

Chapter 4: Northern Spotted Owl Habitat and Populations: Status and Threats

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Introduction

The northern spotted owl (*Strix occidentalis caurina*) was listed as threatened under the Endangered Species Act in 1990 (USFWS 1990). Providing adequate amounts of suitable forest cover to sustain the subspecies was a major component of the first recovery plan for northern spotted owls (USFWS 1992) and a driver in the basic reserve design and old-forest restoration under the Northwest Forest Plan (NWFP, or Plan) (USDA and USDI 1994). The reserve design included large contiguous blocks of late-successional forest, which was expected to be sufficient to provide habitat for many interacting pairs of northern spotted owls. As such, the selection of reserves generally favored areas with the highest quality old-growth forests, but some areas of younger forest were also included with the expectation that they would eventually develop suitable forest structure characteristics and contribute to spatial patterns that would sustain spotted owl populations.

Northern spotted owls are now one of the most studied birds in the world. Much of the research and interest in spotted owls stem from the economic and ecological implications surrounding management for the subspecies. Courtney et al. (2004) and the U.S. Fish and Wildlife Service (USFWS 2011b) completed comprehensive reviews and syntheses of scientific information regarding the status, ecology, and threats to the northern spotted owl. In the 10-year science synthesis of the NWFP, Raphael (2006) detailed the expectations and observations for northern

spotted owl populations and suitable forest types under the Plan. Here we provide a 20-year synthesis of northern spotted owl science and review key information concerning the ecology and expectations for conservation of northern spotted owls under the NWFP. We build upon previous syntheses and address guiding questions by focusing on the scientific understanding accumulated from 2005 to 2016 on the ecology, conservation, and management of northern spotted owls. We also provide an overview of the main scientific debates surrounding conservation and management of northern spotted owls. We discuss the distinction between associated forest cover types and the relative value of habitat in different forest types for the subspecies. Where needed, we review and draw inference from research related to Mexican spotted owls (*S. o. lucida*) and California spotted owls (*S. o. occidentalis*), but keep the focus of this synthesis on published literature specific to northern spotted owls (spotted owl hereafter).

Major threats to spotted owls identified at the time of design and initial implementation of the NWFP and species recovery plan included the effects of past and current timber harvest, loss of old forest to wildfire, and competition with rapidly encroaching barred owls (*Strix varia*) (USDA and USDI 1994, USFWS 1992). Studies of associations between spotted owls and forest cover published since 2005 have reinforced previous work indicating a strong association of nest and roost sites with older forest conditions and a wider range of forest cover types used for foraging and dispersal (Anthony et al. 2006; Carroll and Johnson 2008; Dugger et al. 2005, 2016; Forsman et al. 2011, 2015; Hamer et al. 2007; Irwin et al. 2012, 2013; McDonald et al. 2006; Olson et al. 2005; Sovern et al. 2015). In the southern portions of the range, abiotic environmental factors begin to play larger roles in territorial owl use (Glenn et al. 2017), and at the very southern end of the range (Marin County, California), spotted owls occur at higher densities and tend to nest in a wider variety of forest cover types and ages (Stralberg et al. 2009). The difference in localized spotted owl densities and generalist vegetation associations appear to be driven by the diversity of forest conditions and high prey density prevalent in that landscape.

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Every study that has assessed rangewide population trends of spotted owls found steady declines since standardized monitoring efforts started in 1985 (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011, Franklin et al. 1996). Loss of suitable forest and competitive interactions with barred owls are the primary threats that have contributed to those declines. In the following sections, we review recent information on the status and trends of spotted owl populations and suitable forest, effects of interactions with barred owls, prey ecology, disturbance impacts, climate change, and other threats. We also review population trends and range expansion of barred owls, their habitat and prey, and identify other sensitive wildlife and ecological processes that may ultimately be affected by the invasion of barred owls. We conclude by outlining considerations for management and research needs for spotted owls and forest types most critical to their persistence.

Guiding Questions

We used the following questions received from forest managers to guide our synthesis and focus on relevant spotted owl literature. Following each question, we provide the section that most effectively addresses the question, or if a question could not be adequately addressed because of a lack of published literature on the subject.

1. What is the current understanding about spotted owl population status? Will continuing to implement the NWFP reverse the downward trend in spotted owl populations?
 - Information can be found in the “Population Status and Trends” and “Conclusions and Management Considerations” sections.
2. Is the NWFP maintaining or restoring forest conditions necessary to support viable populations of spotted owls?
 - Despite old-forest loss to wildfire and timber harvest, implementation of the NWFP has been successful for putting federal lands on a trajectory for restoring forest capable of supporting spotted owls on federal lands. Information can be found in the “Habitat Status and Trends,” “Disturbance,” and “Conclusions and Management Considerations” sections.
3. What are the effects of various timber management practices and wildfire on forests used by spotted owls?
 - Information can be found in the “Habitat Status and Trends,” “Disturbance,” and “Research Needs” sections.
4. How is space use by spotted owls affected by timber management? Are there ways to modify management activities (i.e., silvicultural treatments) to benefit spotted owls? How do managed stands compare to untreated forests in terms of use by spotted owls?
 - Information can be found in the “Habitat Status and Trends,” “Disturbance,” “Research Needs,” and “Conclusions and Management Considerations” sections.
5. Do spotted owls use forests following wildfire? If so, how? Do the impacts of treatments that reduce risk of wildfire outweigh the risks of suitable forest loss resulting from wildfire?
 - The short- and long-term response by spotted owls to wildfire remains largely unknown, and scientific debate remains. We were unable to fully address this question, but do provide a synthesis of available literature in the “Habitat Status and Trends,” “Disturbance,” “Research Needs,” and “Scientific Uncertainty” sections.
6. How effective are protections for buffered areas around nest sites in retaining spotted owls across treated landscapes? Are site buffers equally effective as landscape-scale forest management in ensuring species persistence, dispersal, and habitat connectivity?
 - We were unable to address this question fully owing to the lack of published literature, but some information about the effectiveness of buffered management areas can be found in the “Habitat Status and Trends,” and “Forest protection effectiveness” sections.

7. Which provides a higher level of spotted owl persistence: the current spotted owl critical habitat or the NWFP late-successional reserve network?
 - Information can be found in the “Habitat Status and Trends,” and “Forest protection effectiveness” sections.
8. Does treating late-successional stands improve spotted owl persistence when wildfire, insects, disease, and climate change threaten the ability of these forests to provide habitat for spotted owls?
 - Information can be found throughout the chapter in the “Habitat Status and Trends,” “Barred Owls,” “Disturbance,” “Climate Change,” “Other Threats,” “Research Needs,” “Scientific Uncertainty,” and “Conclusions and Management Considerations” sections.
9. What are the effects of barred owls on spotted owls? What is the relationship of wildfires to barred owl encroachment? Can a barred owl management program be effectively implemented at a scale that will have meaningful conservation value for spotted owls?
 - Information about the effects of barred owls is found in “Barred Owls.” We were unable to adequately address questions about the relationship between barred owls and wildfire, and barred owl management, because of a paucity of literature. In addition, some of this research was ongoing at the time this synthesis was being prepared. We provide further details in “Research Needs, Uncertainties, Information Gaps, and Limitations.”
10. What are the management considerations and research needs for spotted owls?
 - Based on our synthesis of available literature within the context of the guiding management questions we received, we specifically address high-priority information needs in “Research Needs, Uncertainties, Information Gaps, and Limitations.” We conclude the chapter with “Conclusions and Management Considerations.”

Key Findings

Population Status and Trends

Understanding vital rates (e.g., birth, death) and the factors affecting those parameters over time and space can provide crucial information for management and conservation. Since the listing of the spotted owl, demographic rates have been monitored in up to 14 demographic study areas distributed across the spotted owl’s geographic range. Franklin et al. (1996) developed a general framework to estimate demographic parameters and population trends of spotted owls that has been used in subsequent spotted owl population analyses. In the past 10 years, three meta-analyses (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011) documented a continued decline in spotted owl populations throughout their range. Those meta-analyses built upon the Franklin et al. (1996) methods to analyze survival, reproduction, and territory occupancy data that has been collected consistently for nearly three decades.

The number of study areas in which spotted owls have been monitored has changed through time owing to changes in funding and institutional support. Anthony et al. (2006) used data from 14 study areas (1985 to 2003), Forsman et al. (2011) used data from 11 study areas (1985 to 2008), and Dugger et al. (2016) used data from 11 study areas (1985 to 2013) to evaluate survival, fecundity, recruitment, and rate of population change of spotted owls throughout the subspecies’ geographic range (fig. 4-1). Dugger et al. (2016) also investigated territory occupancy dynamics (gains and losses of occupied territories; i.e., local colonization and extinction rates). All three meta-analyses investigated relationships between population demography of spotted owls and the distribution of suitable forest cover types, local and regional variation in climatic conditions, and presence of barred owls. Study areas included in these meta-analyses comprised about 9 percent of the spotted owl’s range, were distributed throughout the geographic range, and were selected to encompass the broad range of forest conditions used by the subspecies.

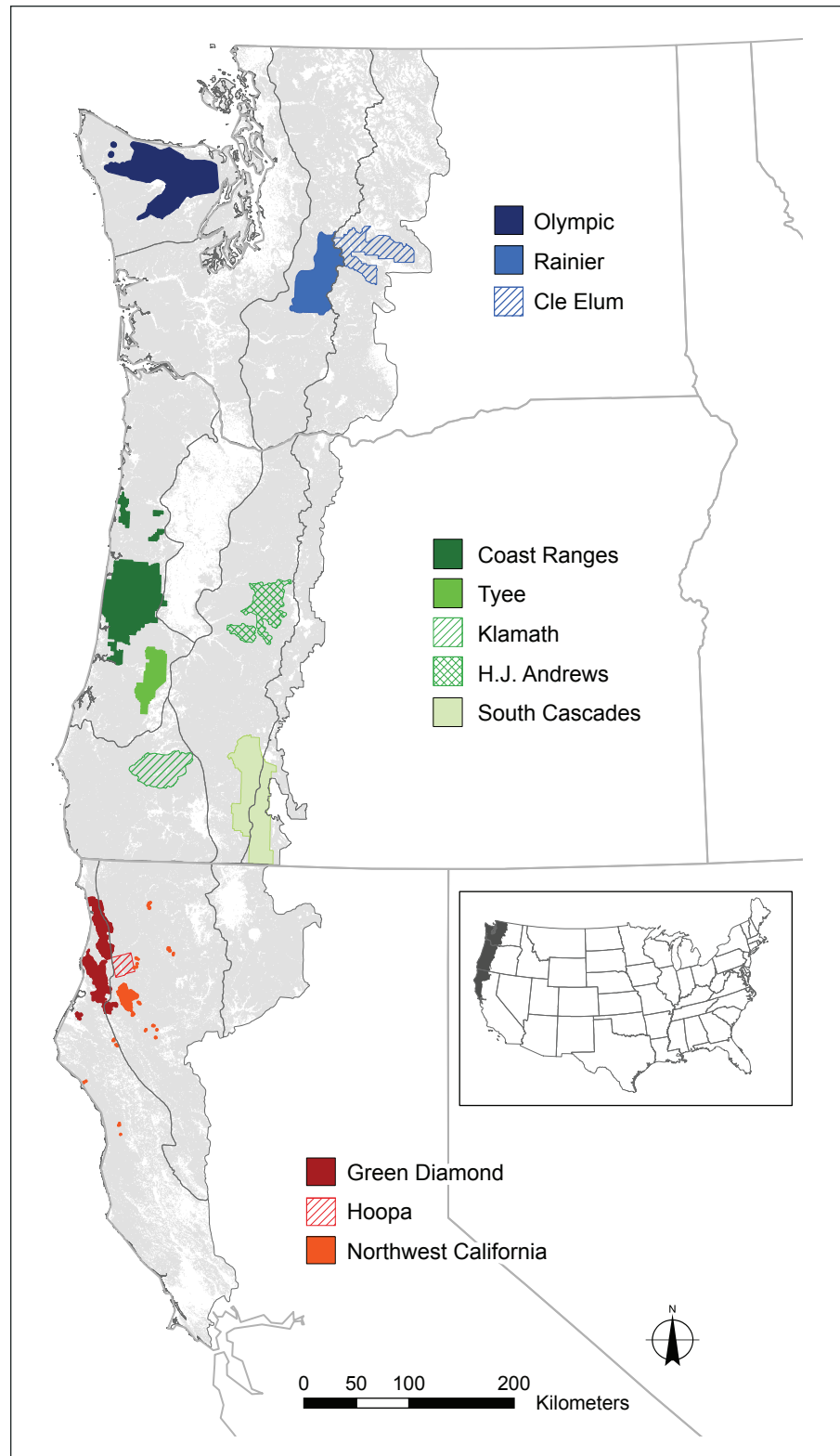


Figure 4-1—Locations of 11 study areas used in the analysis of vital rates and population trends of northern spotted owls, 1985 to 2013 (Dugger et al. 2016).

When the NWFP was developed, populations of spotted owls were estimated to be declining at about 4.5 percent (confidence interval [CI] 1.1 to 7.9) per year (Burnham et al. 1996, USDA and USDI 1994). The population was expected to continue declining for up to 50 years until younger second-growth forest in reserves matured to a point at which it would provide suitable structural conditions for nesting and roosting (Lint 2005, USDA and USDI 1994). During the first 10 years of the NWFP, the overall rate of population decline in Washington was much greater than in Oregon and California (Anthony et al. 2006, Lint 2005). Three study areas in southern Oregon had stable populations during the first decade. Anthony et al. (2006) estimated an annual decline of 3.7 percent (CI = 1.9 to 5.5) across the range, but that analysis included lands outside of the NWFP monitoring area. The eight federal study areas within the boundaries of the NWFP area (i.e., lands under federal management) used for effectiveness monitoring of the NWFP had a decline of 2.4 percent (CI = 1.0 to 3.8) compared to a 5.8 percent (CI = 2.6 to 9.0) decline for

study areas composed primarily of nonfederal lands, suggesting that implementation of the NWFP had a positive effect on the demography of spotted owls (Anthony et al. 2006, Raphael 2006). Forsman et al. (2011) estimated an annual decline of 2.9 percent (CI = 1.7 to 4.0) throughout the northern spotted owl's range, and Davis et al. (2011) estimated an annual decline of 2.8 percent (CI = 1.5 to 4.2) within the eight federal study areas. The most recent meta-analysis indicated that spotted owl populations were continuing to decline throughout the range of the subspecies, and that annual rates of decline were accelerating in many areas (Dugger et al. 2016). The population was declining by about 3.8 percent (CI = 0.1 to 7.5) per year and declines ranged from 1.2 percent to 8.4 percent per year depending on the study area (fig. 4-2) (Dugger et al. 2016). For monitored populations, population change was more sensitive to adult survival than to recruitment (Glenn et al. 2010). Other studies have also documented declines in populations throughout the range of the spotted owl (Farber and Kroll 2012, Funk et al. 2010, Kroll et al. 2010).

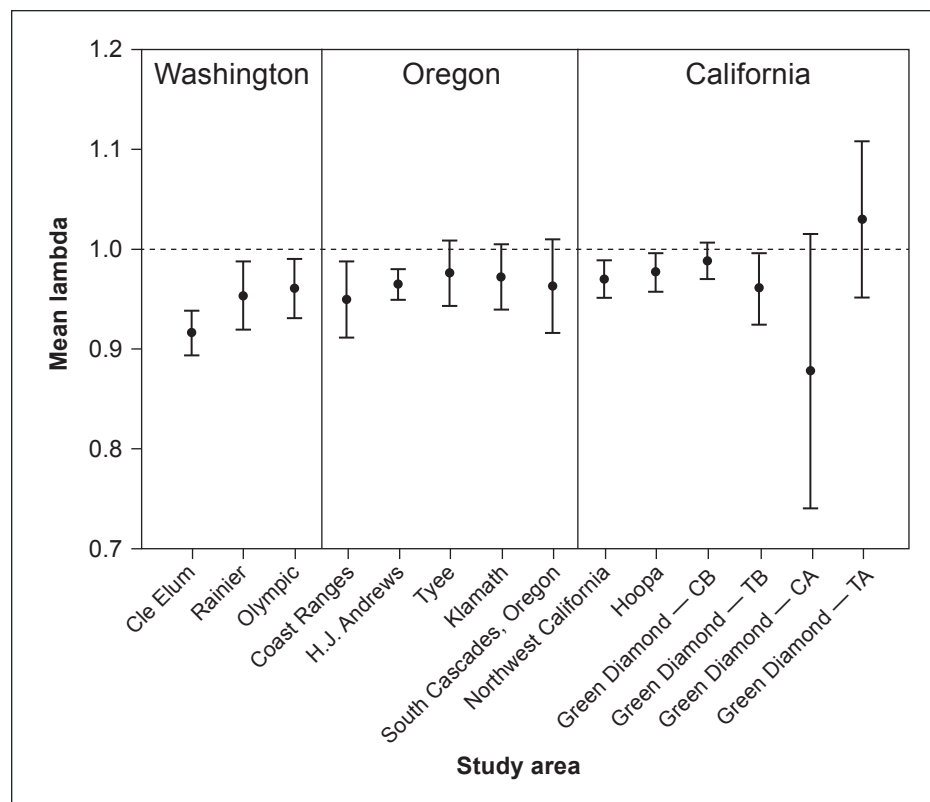


Figure 4-2—Estimated mean rates of population change (mean lambda) and 95 percent confidence limits for spotted owls from 1985 to 2013 at 11 sites: Cle Elum, Rainier, and Olympic, Washington; Coast Range, H.J. Andrews, and Tyee, Klamath, and South Cascades, Oregon; and northwest California, Hoopa, and Green Diamond, California (from Dugger et al. 2016). Estimates for Green Diamond are presented separately for control and treatment areas before (1990 to 2008) and after (2009 to 2013) barred owls were removed on the treatment area (CB = control before removal; TB = treatment before removal; CA = control after removal; TA = treatment after removal) (Diller et al. 2016, Dugger et al. 2016).

Habitat Status and Trends

Background and definitions—

Habitat for a species is an area that encompasses the necessary combination of resources and environmental conditions that promotes occupancy, survival, and reproduction of that species (Morrison et al. 2006). Typical wildlife habitat components include food, water, shelter (including nesting or denning sites), security from predators and competitors, and proper spatial arrangement of those features (Morrison et al. 2006). Although this concept of habitat may seem simple, the ways in which these individual components and animal needs interact in space and time result in very complex relationships (Mathewson and Morrison 2015).

Spotted owl habitat has often been characterized as older forest with large trees and moderate to closed canopy (Courtney et al. 2004, Forsman et al. 1984). Spotted owl site occupancy has repeatedly been shown to be influenced by the presence of these forest conditions (e.g., Dugger et al. 2016), likely because they often provide important habitat components that are suitable for nesting (e.g., cavities or platforms) (Sovern et al. 2011), abundant prey populations (Carey et al. 1992, Forsman et al. 2004, Wilson and Forsman 2013), and security from predators, including other raptors (Forsman et al. 1984, Sovern et al. 2014). An advantage of characterizing spotted owl habitat based on forest structure is that these forest types can be mapped for the entire subspecies' range using remotely sensed data (Davis et al. 2016). Other habitat components like prey abundance, predation risk, and presence of competitors are much more difficult, if not impossible, to map independently. For example, the recent colonization of the range of northern spotted owls by barred owls has confounded efforts to quantify the amount of habitat available for spotted owls because barred owls use similar forest types and can displace spotted owls from those areas (see "Barred Owl" section below).

In addition to availability, the arrangement of habitat components at a variety of scales is also important for understanding spotted owl habitat. Typically, spotted owl habitat is discussed in terms of forest cover types (stand-level forest structure and composition) most suitable for nesting, roosting, foraging, or dispersal (Davis et al. 2016, Lint 2005, Thomas et al. 1990). However, the spatial and temporal

dynamics of suitable forest cover types, and how environmental conditions including climate and topography interact with vegetation patterns, are also important for producing and sustaining habitat for spotted owls (USFWS 2012a, 2012b). For example, Glenn et al. (2017) constructed habitat models using forest cover types and abiotic environmental conditions, and estimated the density of spotted owl territories on a landscape before and after barred owl invasion.

In this chapter, we define spotted owl habitat as those areas with the full suite of resources (e.g., abundant prey, available nest structures) and environmental conditions (e.g., appropriate climate, suitable forest structure, and infrequent presence of barred owls) suitable for occupancy, reproduction, and survival of the subspecies. As such, habitat is more analogous to a species' realized niche rather than the fundamental niche because habitat is more constrained than the availability of a vegetation type and a subset of environmental conditions. All published models of spotted owl habitat fall short of this definition because the distribution of spotted owls in relation to abundant prey is not known, and the distribution of an important competitor—barred owls—is not fully known. Throughout this chapter we distinguish between spotted owl habitat and components of that habitat (e.g., forest cover types used for nesting and roosting) regardless of the terms used in published literature.

Differing concepts regarding habitat definitions have long caused confusion and uncertainty in the interpretation of scientific literature (Bamford and Calver 2014, Hall et al. 1997, Morrison et al. 2006). The differences in how spotted owl habitat is defined and modeled has also caused confusion. The NWFP monitoring program estimates trends in forest types used by spotted owls (Davis and Lint 2005). The Fish and Wildlife Service (USFWS 2012a) modeled suitable forest and considered the amount and spatial arrangement of forests associated with specific life history requirements (e.g., forest types used for foraging in relation to forests used for nesting and roosting), as well as abiotic factors (e.g., slope, climate). The resulting models were used for delineation and designation of what was considered critical habitat (USFWS 2011b). The models of potential spotted owl habitat developed by the NWFP monitoring

program and the Fish and Wildlife Service have important differences that result in different amounts of what is considered suitable forest for spotted owls. Estimates of the amount of suitable forest for spotted owls are highly scrutinized because of the conflict caused by the importance of that forest type for the reproduction and survival of spotted owls and because merchantable large timber is important economically for many of the rural areas where old forest occurs. The different estimates of suitable forest cover for spotted owls resulted in litigation filed in relationship to critical habitat designation. Carpenters Industrial Council et al. vs. Ashe and Salazar (District of Columbia District Court case number 1:2012cv00111 filed January 24, 2012) claimed that the USFWS (2012a) estimate of approximately 18 million ac (7.3 million ha) of suitable forest conditions (they used the term habitat) for spotted owls was an overestimate of 5.9 million ac (2.4 million ha) because previous documents produced by the agency had used estimates of approximately 12.1 million ac (4.9 million ha) as found in (Davis et al. 2011). The 2.4 million ha difference can be explained by an examination of how habitat was defined and modeled in

the different efforts. For example, estimates from Davis et al. (2011) were based on a stand-level designation of forest cover suitable for nesting and roosting (fig. 4-3A), whereas USFWS (2011b) and USFWS (2012a) delineated critical habitat based on a model that included suitable forest stands (Davis et al. 2011) and other landscape components essential for spotted owls at the core-area scale (200 ha) (fig. 4-3B).

The NWFP defined suitable forest for spotted owls as an area with the species of trees, structure associated most commonly with late-successional forest, sufficient area, and adequate food source to meet some or all of the subspecies' life needs, including nesting, roosting, and foraging (USDA and USDI 1994). This definition relied heavily on the work in the Interagency Scientific Committee report (Thomas et al. 1990), which acknowledged the difficulty in defining habitat and chose to characterize the concept based on relative value or suitability of forest stands for spotted owls. Forest cover can be viewed as supporting different spotted owl life functions (e.g., nesting, roosting, foraging) and a suitability gradient in terms of its influence on individual fitness (Thomas et al. 1990). Partitioning of forest cover

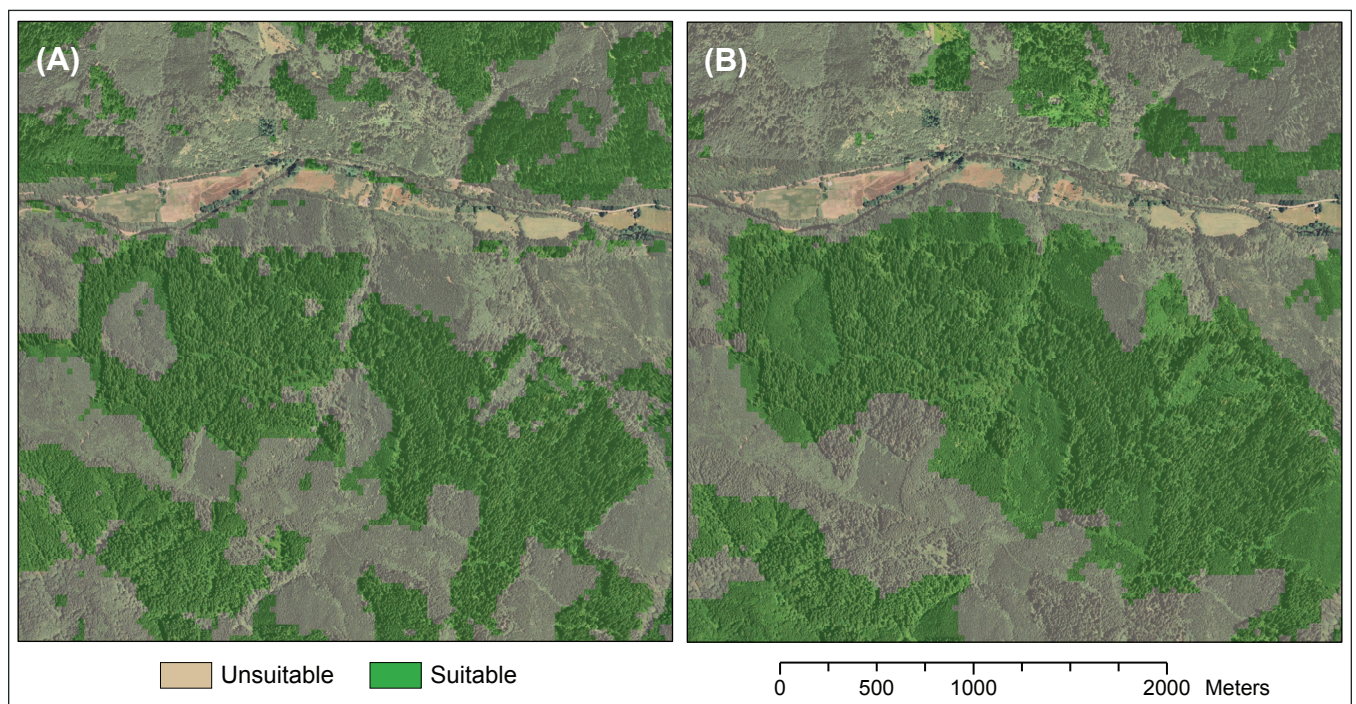


Figure 4-3—Examples of the suitable forest cover at (A) the stand scale developed by the Northwest Forest Plan monitoring program (Davis et al. 2011), and (B) the 200-ha (~250-foot radius) core-area scale used for modeling and delineating critical habitat (USFWS 2012a).

into discrete categories based on established measures of suitability for particular life functions facilitates a common frame of communication and standardization. A monitoring framework to measure relative suitability of forest cover types used by spotted owls was developed as part of a rangewide monitoring program for the subspecies (Davis et al. 2011, 2016; Lint 2005). Monitoring divided a continuous gradient of cover-type suitability into four discrete classes (table 4-1), based on use-versus-availability analyses using documented territorial pair locations. The unsuitable class was used for nesting and roosting by spotted owls less than expected by chance based on availability, the marginal class was used in proportion to its availability, the suitable class was used more often than expected by chance, and the highly suitable class was used much higher than one would expect from chance based on its availability. For monitoring purposes that dates to the life of the NWFP, the suitable and highly suitable classes were combined into a single class to identify forests that were most strongly associated with nesting and roosting locations. Thomas et al. (1990) characterized highly suitable forest cover as forests that include a multilayered, multispecies canopy dominated by large (>30 inch diameter at breast height [d.b.h.]) conifer trees; an understory of shade-tolerant conifers or hardwoods; moderate to high (60 to 80 percent) canopy cover (they used

the term closure, but by definition they had described cover) (Jennings et al. 1999); substantial decadence in the form of large, live coniferous trees with deformities (e.g., cavities, broken tops, and dwarf mistletoe infections); numerous large snags; large accumulations of logs; and other woody debris. The unsuitable or marginal classes do not imply unimportance to spotted owls because the classification was restricted to describe only suitability for nesting and roosting activities by spotted owls. The marginal class is likely important for supporting dispersal, foraging, and nonbreeding (i.e., floater) individuals that can replace adult mortality and dispersal at nesting territories. Likewise, unsuitable and marginal classes may be important forest types for many prey species used by spotted owls. Forests that are suitable for nesting and roosting have similar characteristics throughout the range of spotted owls, but the path of development to those conditions typically differ based on the fire regime within the area (chapter 3; table 4-2, fig. 4-4).

Thomas et al. (1990) defined forest suitable for dispersal as having ≥11 inch (28 cm) d.b.h. trees and ≥40 percent canopy cover occurring on ≥50 percent of a 36 mi² township; this definition became known as the 50/11/40 rule. Analyses of movement data of spotted owls suggest that most (90 percent) dispersal occurred through landscapes meeting these criteria and are generally considered

Table 4-1—General descriptions of forest cover type classes used to estimate the amount of suitable forest available for nesting and roosting by spotted owls.

Cover type class	General description
Unsuitable	Younger forests or older forests with higher basal area of pine or high-elevation tree species or more open canopies. Usually smaller than average tree diameters, and lacking the presence of residual large trees and multiple canopy layers.
Marginal	Usually mid-seral forests, but can also be older forests lacking large-diameter trees, having simpler stand structure, or primarily composed of pine or high-elevation tree species.
Suitable	Forest stands older than 125 years of age, except in the California redwoods, where younger stands are used. Average tree diameters are usually above 20 inches (50 cm) d.b.h., with the presence of at least a few large trees exceeding 30 inches (75 cm) d.b.h. Canopy cover is usually greater than 60 percent, and the stand has multiple canopy layers.
Highly suitable	Typically forests 150 and 200 years of age or older. Average tree diameters often in excess of 30 inches (75 cm) d.b.h. except in drier portions of the range, where tree ages and sizes are typically smaller (e.g., 120 years and 24 inches). Canopy cover is usually in excess of 70 percent, and the stand has multiple canopy layers with high diversity of tree sizes.

d.b.h. = diameter at breast height.
Source: Davis et al. 2016.

Table 4-2—General descriptions of how forest cover types suitable for nesting and roosting by spotted owls typically develop within four general fire regimes within the Northwest Forest Plan (NWFP) area

Fire regime	Typical development of suitable nesting/roosting forest
Infrequent—high severity (Coast Range, fig. 4-4)	Large contiguous patches that form following infrequent, yet very large, high-severity wildfires. Once established, these large patches persist for long periods until the next large high-severity wildfire. Immediately following a large wildfire, large areas of the landscape are unsuitable for nesting and roosting for decades until closed canopies redevelop in areas that had remnant tree structures that could serve as nest trees. During this period, fine-scale gaps created by root-rot pockets, windstorms, landslides, and other small-scale processes produce complex stand structure. Complex structure sometimes does not develop over large areas for several decades following a wildfire. Produces the largest diameter and tallest nest trees; nests are usually in cavities or broken tops.
Moderately frequent—mixed severity (West Cascades, fig. 4-4)	Abundant to moderately abundant on the landscape, but very well connected across the landscape owing to the lack of extremely large high-severity wildfire patches. High-severity wildfire created smaller patches of complex early-seral forest cover type within an otherwise older forest matrix. Through time, these wildfire-created patches produced complex forest structure at the stand scale and a diverse mosaic of seral stages at the landscape scale.
Frequent—mixed severity (Klamath Mountains, fig. 4-4)	Moderately abundant on the landscape but more confined to topographic positions that functioned as wildfire refugia (e.g., lower slopes, north aspects, etc.). These areas allowed for the development and persistence of large trees required for nesting structures. In the Klamath Mountains and California Coast Range physiographic provinces, evergreen hardwoods (e.g., tanoak) are an important component that increase the suitability of use in these stands. In addition to forest stand structure and species composition, climate, and topography are important predictors of use by spotted owls.
Very frequent—low severity (East Cascades, fig. 4-4)	Not naturally abundant within the NWFP area; primarily restricted to the east side of the Cascade Mountains and eastern parts of northern California. Occurred historically in areas where the topography or soil conditions created a productive environment suitable for the development of large Douglas-fir and grand fir. Once established, these closed-canopy, structurally complex forest cover conditions can be relatively resistant to most fires, but burn with high severity under extreme weather conditions (chapter 3).

capable of supporting dispersal (Davis et al. 2011, 2016; Forsman et al. 2002; Lint 2005). However, the Thomas et al. (1990) 50/11/40 hypothesis was not based on juvenile resource selection data and remains largely untested. Only two studies (Miller et al. 1997, Sovern et al. 2015) have empirically studied forest-type selection during juvenile dispersal. Both studies found that juveniles strongly select for old forest with closed canopy (>70 percent canopy cover) and large-diameter trees (>20 inch d.b.h.), which are similar forest conditions selected by adult spotted owls for nesting and roosting (Miller et al. 1997, Sovern et al. 2015). Given the importance of forest cover classified as suitable for

nesting and roosting to juvenile dispersal, the canopy cover recommendations of Thomas et al. (1990) are unlikely to be sufficient to facilitate juvenile movements on the landscape. Sovern et al. (2015) suggested that stands managed for dispersing spotted owls should be at least 80 percent canopy cover and have large average tree diameter.

Both the nesting/roosting and dispersal maps of suitable cover types produced by the NWFP monitoring program were designed to match the conceptual descriptions of forest vegetation components defined by Thomas et al. (1990) and used at the time of the NWFP development. Mapping of forests used by spotted owls is continuing to

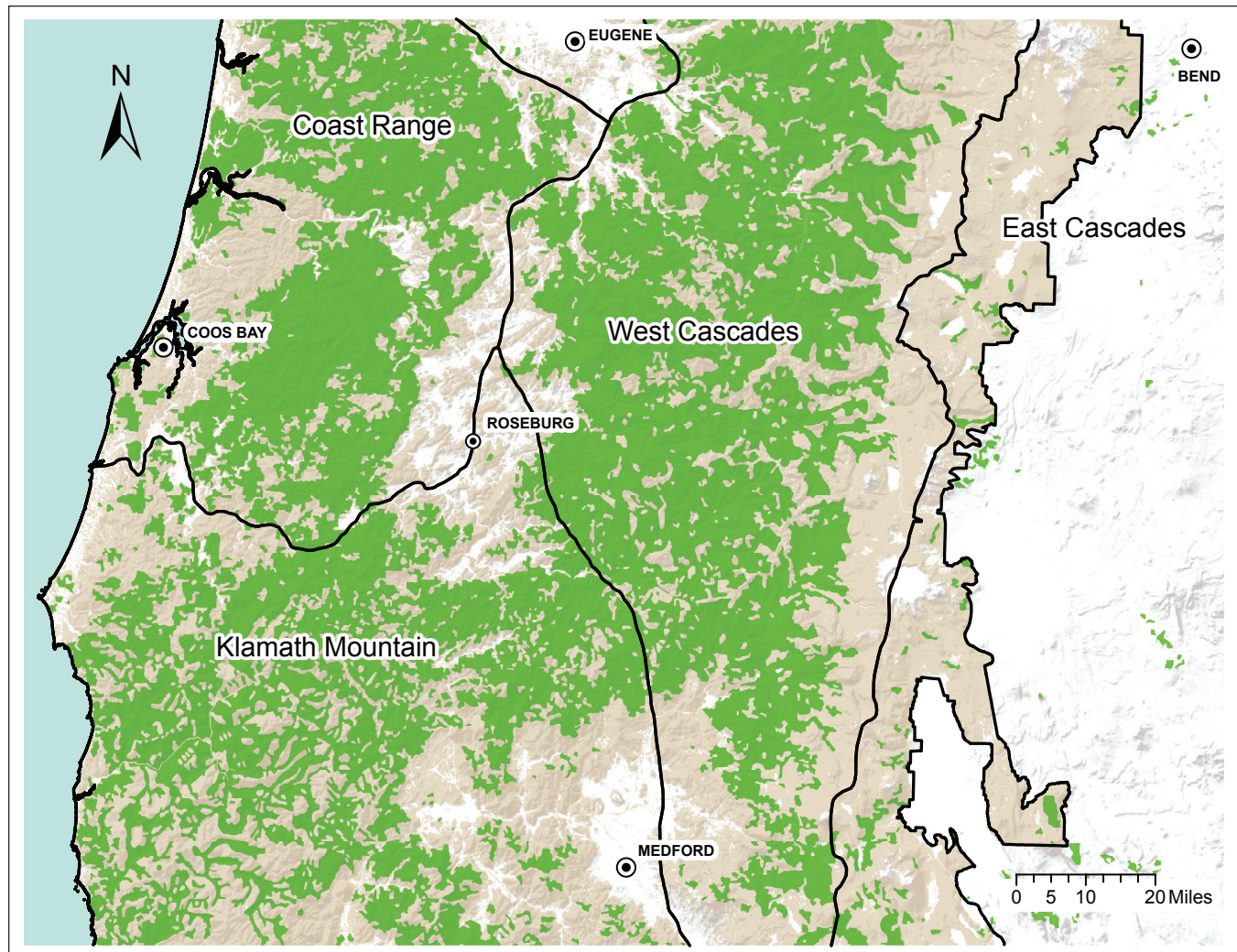


Figure 4-4—Differing historical patterns of old-growth Douglas-fir and mixed-conifer forest (green shaded areas) in west-central Oregon (Andrews and Cowlin 1940) within four areas with different fire regimes (Coast Range, infrequent—high severity; West Cascades, moderately frequent—mixed severity; Klamath Mountains, frequent—mixed severity; East Cascades, very frequent—low severity).

evolve (Ackers et al. 2015). For example, recent maps of suitable forest types (e.g., Glenn et al. 2017; USFWS 2011b, 2012a) differed from the original monitoring maps in that they factored in the spatial arrangement of discrete forest cover types (e.g., nesting, roosting, foraging) as well as abiotic factors (e.g., slope, topographic position, etc.) to produce maps describing a more comprehensive view of suitable forest (i.e., potential habitat). However, even the most recent efforts are not complete models of spotted owl habitat because they lack the impact of prey and barred owls on restricting distribution by limiting access to otherwise suitable forest for spotted owls. An important need is

a better understanding and mapping of the differences between the potential and realized habitat for spotted owls. This is discussed in the “Research Needs, Uncertainties, Information Gaps, and Limitations” section below.

Patterns of change—

Federal vs. nonfederal lands—Davis et al. (2016) estimated that there were about 12.6 million ac (5.1 million ha) of suitable nesting and roosting cover type distributed across the spotted owl’s geographic range at the time of NWFP development (1993), the majority (73 percent) of which occurred on federal lands. By 2012, suitable nesting/roosting forest

cover decreased to 12.1 million ac (4.9 million ha) (74 percent occurring on federal lands), resulting in an overall net change of -3.4 percent. Net decreases were -1.5 percent on federal lands (primarily caused by wildfire) and -8.3 percent on nonfederal lands (primarily caused by timber harvest). During those two decades, forest cover suitable for dispersal decreased from 26.2 to 25.7 million ac (10.6 to 10.4 million ha) (-2.3 percent net change) on all lands. On federal lands, forest cover suitable for dispersal increased by 2.2 percent, and it decreased by 8.6 percent on nonfederal lands (Davis et al. 2016). Gains occurred because of forest succession, whereas losses were primarily a result of wildfire, disease, and timber harvest (Kennedy et al. 2012).

Timber harvest accounted for the majority (63 percent) of the losses across all lands. The vast majority of losses on nonfederal lands was caused by timber harvest (94 percent), whereas timber harvests accounted for 18 percent of total losses on federal lands (Davis et al. 2016). In Washington alone from 1996 to 2004, most (85 percent) of the timber harvest that resulted in lost forest cover suitable for nesting and roosting of spotted owls occurred on private lands (Kennedy et al. 2012, Pierce et al. 2005). Following timber harvest, wildfire was the next largest cause of loss (31 percent of total losses), which was 73 percent of the losses on federal land and only 3 percent of the losses on nonfederal land.

Moist vs. dry forests—Primary causes of loss differed by ecoregion and forest type. The loss of nesting and roosting forest cover from wildfire occurred primarily in drier, fire-prone portions of the spotted owl's geographic range (i.e., northern California, southern Oregon, and eastern Cascade Range). Losses owing to insects and disease (and other natural disturbances) was the next most significant disturbance and mainly occurred in the eastern Cascades of Washington and Oregon (Davis et al. 2016, Kennedy et al. 2012).

Recruitment of forest cover suitable for nesting and roosting by spotted owls was estimated at 257,591 ac (104 288 ha) from 1993 to 2012 (Davis et al. 2016). Most of the gain occurred on nonfederal lands within the redwood (*Sequoia sempervirens*) zone of coastal California (fig. 4-5). On federal lands, the largest net gain (40,385 ac [16 350 ha]) occurred in the eastern Cascades of Oregon, where fire suppression allowed forest succession of Douglas-fir (*Pseudotsuga*

suga menziesii) and grand fir (*Abies grandis*) to develop in areas that historically had frequent low-severity fires and were formerly dominated by open ponderosa pine-dominated forests (*Pinus ponderosa*) (Davis et al. 2016).

Effects of forest change—

Loss of suitable forest cover for nesting and roosting, especially on nonfederal lands, has been an important contributor to declining populations of spotted owls (Dugger et al. 2016). Those spotted owls that had territories with more forest cover associated with nesting and roosting conditions typically had better survival, fecundity, occupancy dynamics, recruitment, and rate of population change (Dugger 2016; Dugger et al. 2005, 2011; Forsman et al. 2011; Seamans and Gutiérrez 2007). For example, Dugger et al. (2005) found that owl territories with the greatest fitness potential were characterized by >50 percent old-forest habitat within a 412-ac (167-ha) circle centered on used nest locations. Relationships among population parameters of spotted owls and older forests vary over different spatial scales (e.g., individual territory vs. study area), and can be independent of, or interact with, the presence of barred owls. Concentrated areas of older forest suitable for nesting and roosting, or increased amounts of heterogeneity (i.e., mixture of conditions used for foraging), have positive effects on the vital rates of spotted owls (Dugger et al. 2016, Forsman et al. 2011, Franklin et al. 2000, Olson et al. 2004).

In some landscapes, fragmentation of older forest can have negative or positive effects on spotted owl occupancy depending on the scale of fragmentation and edge characteristics. Schilling et al. (2013) found that spotted owls had decreased survival and increased home-range size with increased forest fragmentation in southwestern Oregon. In Washington, territory-level extinction rates decreased with increased amount of late-seral edge, and colonization decreased with more late-seral patches within a territory (Sovern et al. 2014). It is also important to consider spatial scale, and level of contrast between edge, when assessing the influence of forest edges on foraging and space use by spotted owls. Comfort et al. (2016) found that spotted owls radio-marked in southern Oregon were negatively associated with hard edges (high contrast in forest structure and height) at a fine scale (telemetry location), but showed a lack

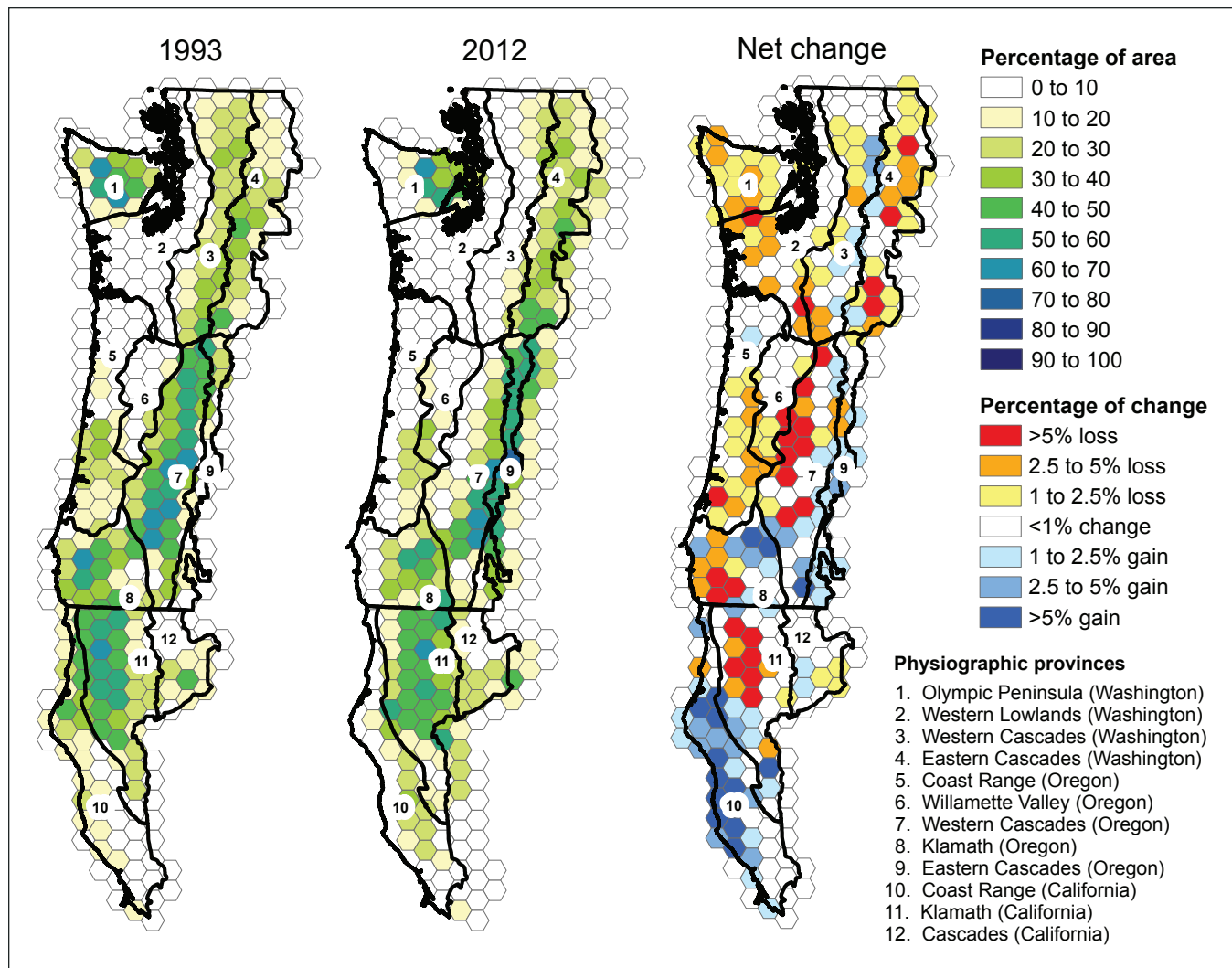


Figure 4-5—Loss and recruitment of forest types suitable for nesting and roosting by spotted owls in 1993 versus 2012, based on change in percentage of cover estimated within 18.6 mi (30 km) (center to center) hexagons across the Northwest Forest Plan area.

of negative response to hard edges at broader scales (territory or home-range scales). At least at the territory scale, heterogeneity can contribute to accessibility to different forest types. Regardless of spatial scale, spotted owls were positively associated with softer, more diffuse edge types created by disturbances such as low- and mixed-severity fire (Comfort et al. 2016). Collectively, these and other studies suggest that spotted owls select for abundant, structurally diverse closed-canopy forest with diffuse late-seral forest edge at the territory scale, and relatively lower fragmentation in nesting areas (Franklin et al. 2000, Olson et al. 2004, Sovern et al. 2014).

Forest protection effectiveness—

The NWFP included a network of large late-successional reserves (LSRs) that were designed to conserve forest for species dependent on older forests (FEMAT 1993). The LSR network was intended to meet the resource needs of many species, but a substantial focus was placed on creating and maintaining forest cover features from a draft recovery plan for the spotted owl (USFWS 1992). LSRs contained enough suitable forest cover to support multiple pairs of spotted owls and were distributed to facilitate movement of spotted owls across their geographic range. Although many of the LSRs contained large areas of older forest, a

significant portion of them were delineated in fragmented landscapes that contained stands of younger forest. Dispersal between LSRs is important for spotted owl conservation, and the NWFP was expected to facilitate that dispersal by designated riparian reserves, retention of green trees in timber harvest units in the matrix, protection of 100 ac (40 ha) areas at known owl sites (managed as LSRs within the matrix), and other administratively withdrawn areas (USDA and USDI 1994). However, these assumptions are largely untested, so it remains unknown if the NWFP is sufficient to facilitate adequate dispersal, which may be a limiting factor of spotted owl populations.

In addition to broad-scale LSRs, forest protections for spotted owls include circles of varying radii centered on used nest locations, within which various amounts of suitable nesting, roosting, and foraging forest cover types are protected. For example, the Fish and Wildlife Service developed guidelines for consultation under section 7 of the Endangered Species Act that included a 2.9-km-radius circle (6,424 ac [2600 ha]) around spotted owl nest locations for evaluating “incidental take” for projects affecting suitable habitats (USDA and USDI 1994). The rationale for this circle size was developed based on preliminary analysis of the median home-range size of radio-marked spotted owls. States also developed rules for state and private forestry practices to protect spotted owl nest sites. For example, the 2006 Washington State Forest Practices Board Rules called for protection of 40 percent cover of suitable nesting and roosting forest within a 6,422 ac (2600 ha) circle around nest sites (WAC 222-10-041). Forsman et al. (2015) suggested that level of protection would not be sufficient because spotted owl home ranges contained more suitable forest cover than would be protected under the Washington forest practices rules. Furthermore, new methods for delineating owl territories (e.g., Thiessen polygons) used by Dugger et al. (2016) provide better representations of the territory.

At the time LSRs were delineated, it was estimated that they contained on average 43 percent older forest (USDA and USDI 1994). The expectation was that all LSRs would eventually fill in and achieve the 60-percent-or-greater area threshold needed to support multiple

breeding pairs and collectively would facilitate spotted owl population recovery. The success of meeting that threshold depends on the frequency, severity, and spatial extent of disturbance (e.g., wildfire, timber harvests), as well as the rate of forest succession, and interactions among these processes on forest recruitment (chapter 3). As of the most recent monitoring report (Davis et al. 2016), the rangewide estimate for suitable nesting/roosting forest cover in LSRs was an average of 42.4 percent in 1993. As of 2012, this average decreased to 42.0 percent. Larger LSRs ($\geq 10,000$ ac) averaged 45.0 percent, decreasing to 44.5 percent by 2012. These losses were due mainly to wildfire and exceeded the regional-scale expected rate of loss (2.5 percent per decade) (FEMAT 1993). Most of the losses of nesting and roosting forest cover have been in the more fire-prone portions of the spotted owl’s range (Davis et al. 2011, 2016). For example, within LSRs and other reserves (e.g., administratively withdrawn, wilderness areas, etc.) in the Klamath Mountains physiographic province, losses were as high as 18.9 percent between 1993 and 2012 (fig. 4-5), and largely the result of the 2002 Biscuit Fire, which burned 494,000 ac ($>200,000$ ha).

Forest cover trends on federal lands during the next two to three decades are expected to benefit spotted owls because significant recruitment of suitable nesting/roosting forest cover is expected to offset many pre-NWFP losses (chapter 3) (Davis et al. 2016). However, this expectation is based on current rates of harvest and wildfire occurrence on federal lands, which may change depending on future forest plan revisions and the predicted increased spatial extent, frequency, and severity of wildfires due to climate change (chapter 2) (Jones et al. 2016, Westerling et al. 2006). In addition, competitive pressure from established barred owls (see below) has raised uncertainties about whether recruitment of suitable forest cover will be enough to conserve spotted owls over the long term. If spotted owls are to persist in LSRs under competitive pressure from barred owls, it will likely be only in localized areas that support few barred owls. However, it remains doubtful if there are any areas where spotted owls hold a competitive advantage over barred owls (Pearson and Livezey 2007, Singleton 2013, Wiens et al. 2014).

The potential effects of climate change add to the uncertainty of how competitive dynamics with barred owls and availability of suitable habitat will affect spotted owls in the future. Carroll et al. (2010) used a climatic niche modeling approach to evaluate the regional system of LSRs for resiliency to climate change for providing necessary resources of species associated with old forest. They developed distribution models integrating climate data with vegetation variables for a large suite of species, including the spotted owl. The LSRs functioned better than expected by chance for capturing all of the species, but community composition and interspecific interactions were also important to consider in evaluating effectiveness of the reserves. A network of fixed reserves with a high level of climatic and topographic heterogeneity (i.e., designed for resilience) has an increased likelihood of retaining the biological diversity of old-forest ecosystems under climate change. Under this scenario, even those species with limited dispersal capability are able to colonize future habitat. Carroll et al. (2010) projected a northward and higher elevation movement of suitable forest for spotted owls; therefore, the current fixed system of LSRs may not have enough climatic and topographic heterogeneity to be adequate for spotted owls into the future. Other reserves designated before the NWFP, such as parks and wilderness areas, may become increasingly important for the subspecies' persistence. LSRs successfully protected areas with greater biological importance for spotted owls when the NWFP was developed, but in the face of climate change, it may be necessary to have another evaluation and planning phase that results in a reserve system designed for more robust resilience (Carroll et al. 2010) (see chapter 3 for more discussion of alternative reserve designs), especially in the dry forest zone where management for ecosystem and spotted owls may not be compatible at stand and small landscape scales (chapter 12). Even with relatively little modification in response to climate change, suitable forest conditions on the east side and southern portions of the range are at risk of losses. Dense, multilayered forests in the dry forest zone are vulnerable to a host of mortality forces, especially wildfire (see chapters 3 and 12).

Barred Owls

Barred owl range expansion and population trends—

Competition with established populations of barred owls has emerged as a much more prominent and complex threat to the long-term persistence of the spotted owl than was anticipated during the development of the NWFP. Once confined to forests of eastern North America, the barred owl is a medium-size, ecologically similar species whose newly extended geographic range now completely overlaps that of the northern spotted owl (Gutiérrez et al. 2007, Livezey 2009). Newly colonizing barred owls in the Pacific Northwest have been classified as native invaders—species that, under the influence of events such as climate change or human modifications to the landscape, have become invasive by expanding their populations into new areas (Carey et al. 2012, Valéry et al. 2009, Wiens et al. 2014). The range expansion of barred owls in western North America is well documented (Dark et al. 1998, Dunbar et al. 1991, Kelly et al. 2003, Livezey 2009, Taylor and Forsman 1976). Initial colonization of different regions by barred owls was variable, but barred owls now appear to co-occupy and outnumber spotted owls throughout the entire range of the threatened subspecies (Dugger et al. 2016, Pearson and Livezey 2003, Singleton et al. 2010, Wiens et al. 2011, Yackulic et al. 2012). Barred owls have also invaded the range of the California spotted owl in the Sierra Nevada (Seamans et al. 2004). The cause of this range expansion is unknown, but landscape changes facilitated by European settlement or historical changes in climate are factors that may have enabled barred owls to expand their range from eastern to western North America (Livezey 2009, Monahan and Hijmans 2007).

With few exceptions, barred owls have not been systematically surveyed in the Pacific Northwest, and the majority of information on their distribution and population trends is limited to incidental observations during surveys of spotted owls (Dugger et al. 1991, 2016; Gutiérrez et al. 2007; Wiens et al. 2011). Despite this shortcoming, incidental field data show a rapid increase in barred owls as they expanded their populations westward and southward into the range of the spotted owl (fig. 4-6) (Dugger et al. 2016). Studies focused on barred owls found much higher densities than estimates based on incidental field observations

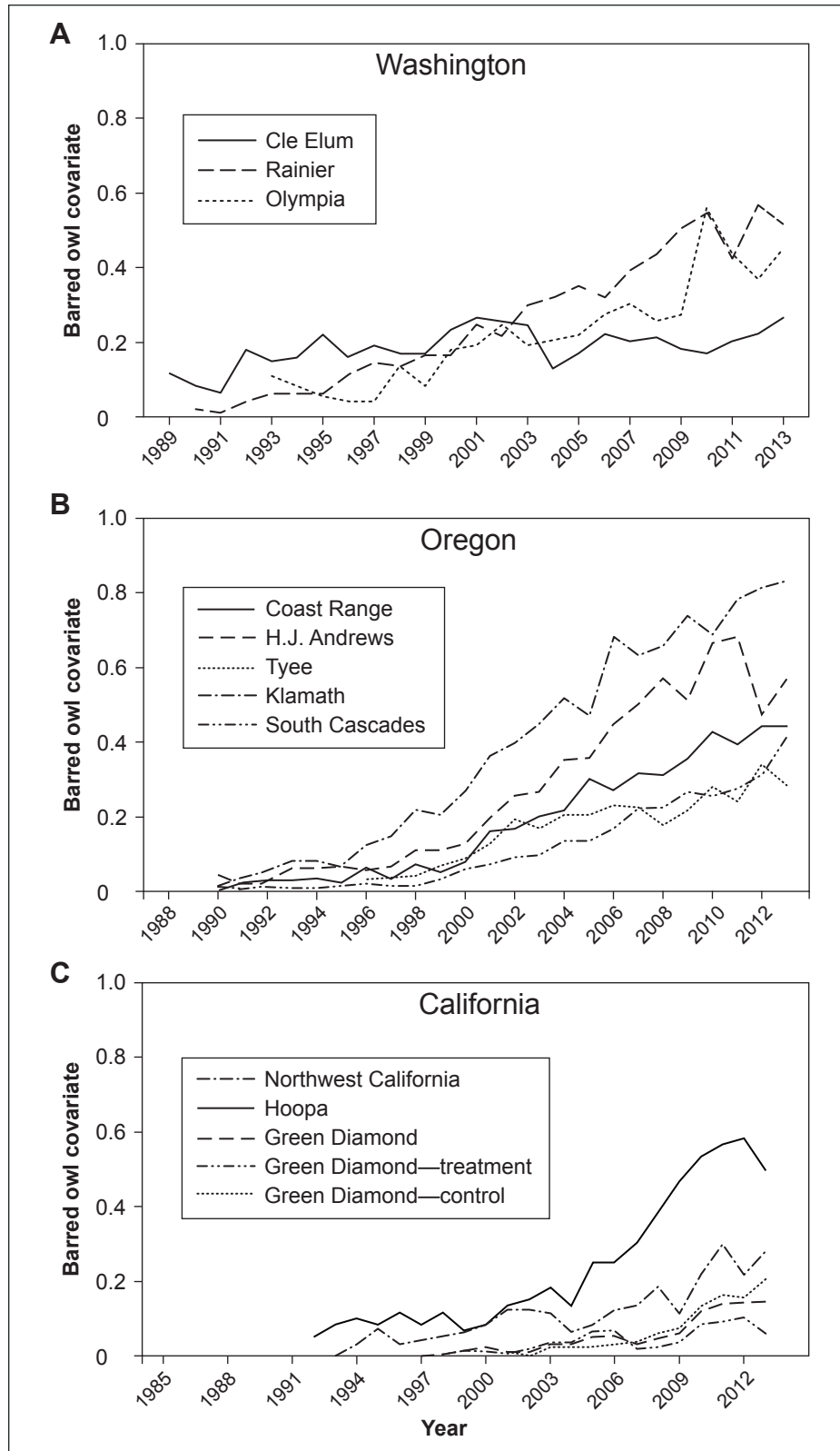


Figure 4-6—Annual increase in the proportion of spotted owl territories with detections of barred owls at (A) three sites in Washington, (B) five sites in Oregon, and (C) three sites in California from 1985 to 2013 (Dugger et al. 2016). Estimates for Green Diamond are presented separately for control and treatment areas and after (2009 to 2013) barred owls were removed from the treatment area from 2009 to 2013.

(Hamer et al. 2007; Singleton et al. 2010; Wiens et al. 2011, 2014; Yackulic et al. 2012, 2014). For example, Wiens et al. (2011) conducted surveys of barred owls during 2009 in the Oregon Coast Range and identified approximately 11 territorial pairs of barred owls per 100 km² (39 mi²; 3 to 8 times higher density than spotted owls) with 89 percent of the landscape occupied, which peaked on publicly owned lands with greater amounts of mature and old coniferous forest. More recent (2015–2016) surveys of barred owls indicate an even greater probability of landscape occupancy in the Oregon Coast Range (~0.94) (Wiens et al. 2017). The degree to which the colonizing population of barred owls has reached carrying capacity within the geographic range of the spotted owl is currently unknown, but studies are underway that can help address this uncertainty (e.g., Wiens et al. 2017). Barred owl populations may continue

to increase depending on the capacity of available habitat and food resources, which varies regionally with forest composition and latitudinal changes in prey communities and climate.

Barred owl effects on spotted owls—

Compared to spotted owls, barred owls are slightly larger (Gutiérrez et al. 2007), have more diverse diets (Hamer et al. 2001, Wiens et al. 2014), and use a broader range of forest conditions for nesting (Herter and Hicks 2000, Livezey 2007, Pearson and Livezey 2003) and foraging (Hamer et al. 2007, Singleton 2015, Singleton et al. 2010, Weisel 2015, Wiens et al. 2014). Barred owls also have higher annual survival (fig. 4-7), higher reproductive output, and, in most areas, use much smaller home ranges than spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). The exception is in northern California,

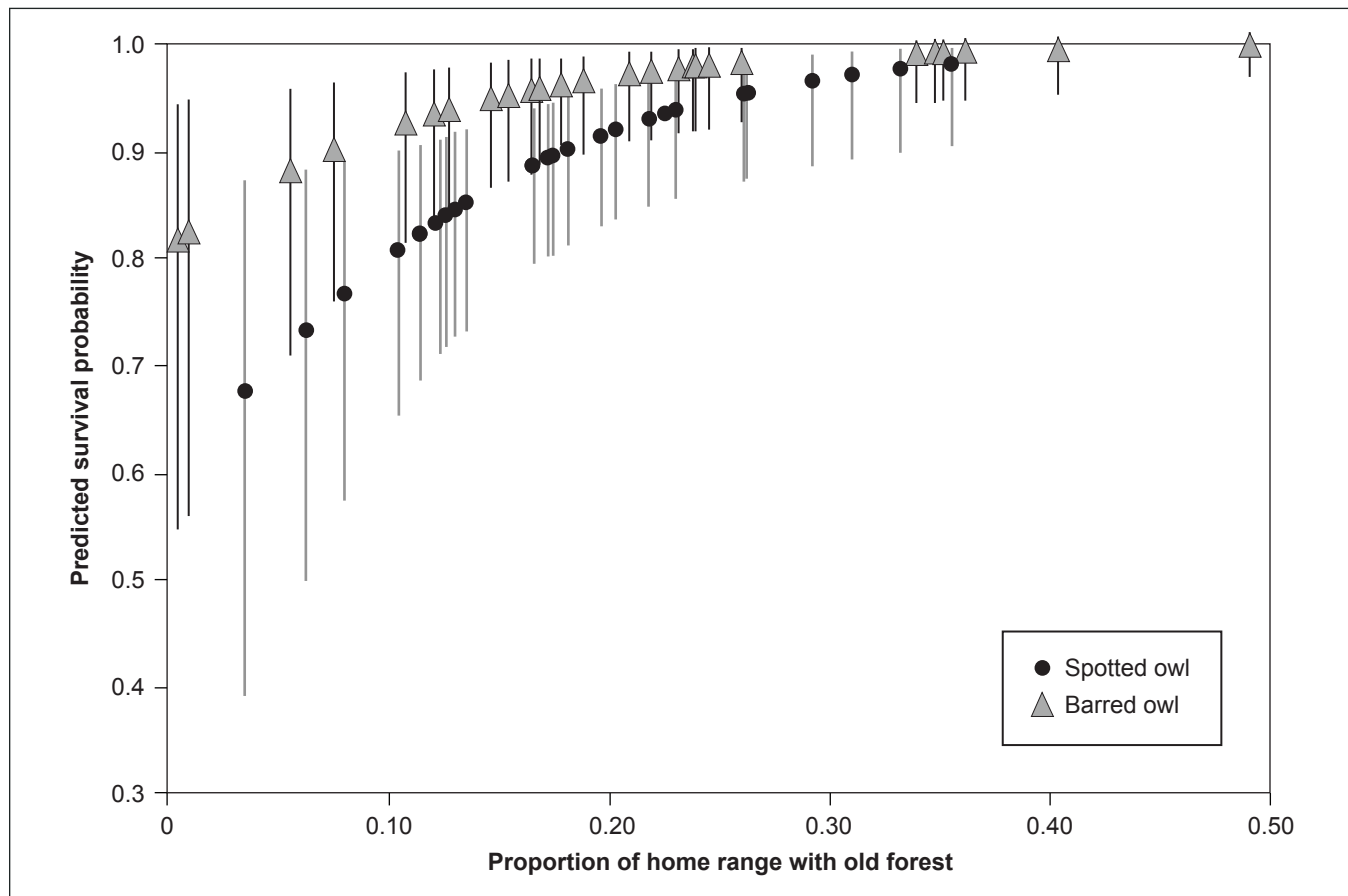


Figure 4-7—Survival (with 95-percent confidence limits) of individual adult barred owls and spotted owls increased with increasing amount of old forest (≥ 120 years) conifer forest within their home ranges in the Oregon Coast Range (Wiens et al. 2014).

where the two species used relatively small home ranges of similar size (Weisel 2015). Barred owls also defend their territories more aggressively than spotted owls (Van Lanen et al. 2011), which can result in increased mortality of spotted owls from agonistic interactions and direct killing of spotted owls by barred owls (Leskiwand Gutiérrez 1998, Wiens et al. 2014).

The dramatic increase in populations of barred owls since implementation of the NWFP has significant implications for management of forests inhabited by spotted owls. Several lines of evidence indicate that increases in the abundance of barred owls has had a strong and negative impact on spotted owls. Increasing abundance of barred owls has been documented to have the following effects on spotted owl populations:

1. Occupancy of historical spotted owl territories is lower (fig. 4-8) (Bailey et al. 2009, Dugger 2016, Dugger et al. 2011, Kelly et al. 2003, Kroll et al. 2010, Olson et al. 2005, Sovern et al. 2014; Yackulic et al. 2014).

2. Apparent survival is lower (Anthony et al. 2006, Diller et al. 2016, Dugger et al. 2016, Forsman et al. 2011, Glenn et al. 2011a).
3. Reproduction is lower (Dugger et al. 2016, Forsman et al. 2011, Olson et al. 2004).
4. Population size declines more rapidly (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011).
5. Hybridization between the species is increased (Barrowclough et al. 2005, Dark et al. 1998, Gutiérrez et al. 2007, Haig et al. 2004, Hamer et al. 1994, Kelly and Forsman 2004).
6. Detection rates during surveys are lower (Bailey et al. 2009, Crozier et al. 2006, Dugger et al. 2011, Dugger et al. 2016, Kroll et al. 2010, Olson et al. 2005, Sovern et al. 2014, Yackulic et al. 2014).

Moreover, studies of competitive interactions and resource partitioning showed that barred owls can directly alter the movements, resource use, and reproduction of spotted owls (Wiens et al. 2014). Barred owls also display demographic superiority over spotted owls; annual rate of

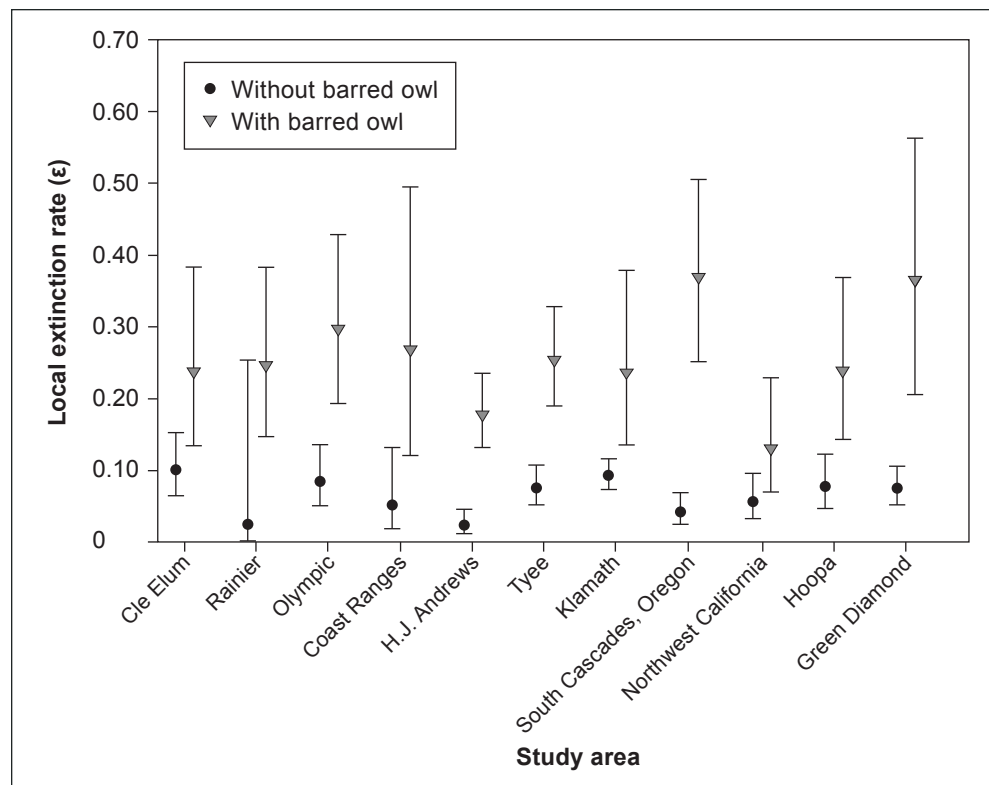


Figure 4-8—Mean annual local extinction rates (with 95 percent confidence limits) for northern spotted owls on 11 study areas in Washington, Oregon, and California relative to with (gray triangles) and without (black circles) the presence of barred owls (Dugger et al. 2016).

survival was greater for barred owls (0.92 ± 0.04) than for spotted owls (0.81 ± 0.05), and mean reproductive output of barred owl pairs was 4.4 times greater than that observed for spotted owls over 3 years in western Oregon (Wiens et al. 2014). More recently, studies in California have demonstrated a positive association between removal of barred owls and population trends of spotted owls (fig. 4-2) (Diller et al. 2016, Dugger et al. 2016). Collectively, these studies provide strong evidence that interspecific competition with an increasing number of barred owls, combined with continued loss of potentially suitable forest cover, is contributing to population declines of spotted owls despite widespread conservation of old forest under the NWFP.

Barred owl densities are now thought to be high enough across the range of the spotted owl that, despite the continued management and conservation of suitable forest cover on federal lands, the long-term persistence of spotted owls is in question without additional management intervention (Buchanan et al. 2007, Diller et al. 2016, Dugger et al. 2016, USFWS 2013). In a few cases, populations of spotted owls have responded positively to the removal of barred owls during pilot removal experiments; supporting the hypothesis that along with forest conservation and management, removal of barred owls might slow or reverse local declines in spotted owl populations in some areas (Diller et al. 2016, Dugger et al. 2016). However, the effectiveness and moreover the feasibility of large-scale barred owl removal for conservation of spotted owls remain to be demonstrated, and barred owl removal activities would likely need to be continued for the foreseeable future to maintain low barred owl densities in control areas.

Barred owl habitat and prey—

Barred owls occupy a broader range of forest types and consume a wider variety of prey than northern spotted owls (Livezey 2007), and use a variety of different forest types in the Pacific Northwest, including fragmented mixed-deciduous forest in rural and urban landscapes (Rullman and Marzluff 2014). Hamer et al. (2007) reported that, in the northern Cascade Range of Washington, barred owls tended to use old forest more than expected, but used most cover types in proportion to availability. Compared to spotted owls, barred owls occupied areas at lower elevations

(Hamer et al. 2007). In the eastern Cascades of Washington, Singleton et al. (2010) reported that barred owls typically established their home ranges in areas that had canopy cover more than 72 percent, medium to large trees (tree crown diameter >21 ft [>6.5 m]), low topographic position (<25 percent), and gentle slopes (<11 degrees). Within those home ranges, barred owls used structurally diverse mixed grand fir forest more intensively than open ponderosa pine or Douglas-fir (Singleton 2015). In the Oregon Coast Range, foraging barred owls most often used patches of old (>120 years) conifer forest in addition to riparian-hardwood forests in relatively flat areas (Wiens et al. 2014). In the redwood region of coastal California, barred owls most often used sites with greater understory vegetation height and more hardwood trees, perhaps in response to greater densities of woodrats (*Neotoma* spp.) in these conditions (Weisel 2015). Collectively, these studies showed that barred owls, in areas where they were sympatric with spotted owls, were most commonly associated with relatively gentle slopes in structurally diverse, mature and old-conifer forests or lowland riparian areas containing large hardwood trees. Use of older forest in combination with moist, valley-bottom forest was also consistent with forest associations described for barred owl nesting areas (Buchanan et al. 2004, Herter and Hicks 2000, Pearson and Livezey 2003). Barred owls use the full range of forest types used by spotted owls, and a broader range of forest cover types outside of areas historically occupied by spotted owls. However, systematic studies have yet to quantify the full range of forest conditions that support barred owls in the Pacific Northwest. There are currently no known forest management actions that would benefit spotted owls more than barred owls.

Dietary studies are lacking for barred owls in California, but their diets in Washington and Oregon included a broad variety of small- to medium-size mammals, birds, frogs, salamanders, lizards, snakes, crayfish, snails, fish, and insects (Graham 2012, Hamer et al. 2001, Wiens et al. 2014). Mammalian prey of barred owls primarily included northern flying squirrels (*Glaucomys sabrinus*), woodrats, brush rabbits (*Sylvilagus bachmani*), snowshoe hares (*Lepus americanus*), moles (*Scapanus* spp.), Douglas squirrels (*Tamiasciurus douglasii*), red tree voles (*Arborimus longicaudus*),

red-backed voles (*Myodes californicus*), shrews (*Sorex* spp.), and deer mice (*Peromyscus maniculatus*) (Hamer et al. 2001, Wiens et al. 2014). Although there is substantial geographic variation in diets of barred owls corresponding with differences in prey distributions, northern flying squirrels appear to be a primary contributor to diets in Oregon and Washington (Graham 2012, Hamer et al. 2001, Wiens et al. 2014).

Although there is some evidence that barred owls were more strongly associated with riparian areas than spotted owls, studies clearly indicate a high degree of ecological overlap between the two species, especially in their use of old-growth forests and associated prey species (Hamer et al. 2001, 2007; Singleton et al. 2010; Weisel 2015; Wiens et al. 2014). In the eastern Cascades of Washington, spotted owls used drier midslope areas less likely to be occupied by barred owls, possibly as a mechanism to minimize interactions with barred owls, at least in the near term (Singleton 2013). This pattern reflects displacement of spotted owls by barred owls from highly suitable forest into conditions less favorable to long-term reproduction and survival of spotted owls, a finding consistent with long-term demographic studies of spotted owls throughout the range of the subspecies (Dugger et al. 2016, Forsman et al. 2011, Singleton 2013, Wiens et al. 2014).

In addition to impacts on spotted owls, changes in the abundance and distribution of an apex predator like the barred owl can have cascading effects on prey populations and food web dynamics (Holm et al. 2016, Wiens et al. 2014), as well as populations of other small sympatric owls (Acker 2012, Elliot 2006). Differences in space use, abundance, demography, suitable forest, diets, and behavior collectively suggest that the barred owl is not a direct functional replacement of the spotted owl in old-growth forest ecosystems (Holm et al. 2016, Wiens et al. 2014). As a consequence, additional changes in community structure and ecosystem processes are anticipated as a result of barred owl encroachment into areas managed under the NWFP.

Spotted Owl Prey

Like all predators, spotted owls are dependent on abundant and vulnerable prey. Much is known about the ecology and population demography of spotted owls, but little information exists on how fluctuations in populations of

prey species influence behavior, space use, reproduction, or population growth of spotted owls. Spotted owls in some areas during some periods have had a strong 2-year cycle of high reproduction one year followed by a year of low reproduction (Anthony et al. 2006). One hypothesis for the cycle in reproductive output is variation in prey abundance. However, simple prey relationship models do not explain the highly synchronous and temporally dynamic patterns of spotted owl reproductive performance (Rosenberg et al. 2003). Northern flying squirrels, woodrats, red-backed voles, and red tree voles are the primary prey of spotted owls throughout different regions of the spotted owl's geographic range (Barrows 1980; Bevis et al. 1997; Forsman et al. 1984, 2004, 2005; Hamer et al. 2001; Rosenberg et al. 2003; Wiens et al. 2014; Zabel et al. 1995). None of these studies had data that could be used to examine relationships between annual variation in prey abundance and annual variation in survival or fecundity of spotted owls. Although deer mice are not a primary prey species (<2 percent biomass consumed), one study (Rosenberg et al. 2003) found a positive correlation ($r^2 = 0.68$) between abundance of deer mice and reproductive success of spotted owls.

Abundance and distribution of primary prey species can influence space use by spotted owls. For example, spotted owls more frequently use riparian areas within their home ranges (Wiens et al. 2014), perhaps because the cool microclimates associated with stream drainages may be favorable for thermoregulatory purposes during summer months (Barrows 1981), or more importantly, riparian areas are likely to support a rich diversity of prey (primarily small mammals) used by spotted owls (Anthony et al. 2003, Carey et al. 1999, Forsman et al. 2004). Home ranges of spotted owls tend to be smaller in the southern portion of the subspecies range, where woodrats are the primary prey, as compared to the northern portion of the geographic range, where woodrats are uncommon and northern flying squirrels are the primary prey (Forsman et al. 2005, Zabel et al. 1995). In northern California, southwestern Oregon, and the eastern Cascades, woodrats occur in fairly open forests and at much greater densities compared to northern flying squirrels (Carey et al. 1992; Lehmkuhl et al. 2006a, 2006b; Wilson and Forsman 2013; Zabel et al. 1995). Differences

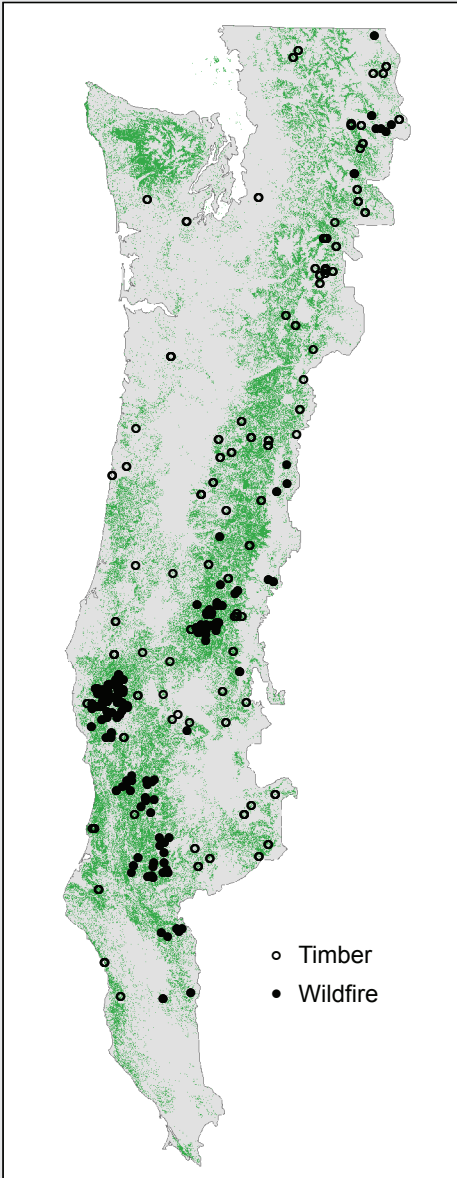
in space use by spotted owls in different portions of their range also relate to regional differences in the availability of prey species. Northern flying squirrels and red tree voles, for example, occur at highest densities in the complex structure of mature Douglas-fir stands with old-growth characteristics, whereas woodrats have greater densities in young stands, along edges, or in brushy areas (Carey et al. 1992, Price et al. 2015, Sakai and Noon 1993, Swingle and Forsman 2009, Walters and Zabel 1995, Zabel et al. 1995). Spotted owls used forest edges to a greater degree when forage consisted primarily of woodrats (Diller et al. 2012), but preferred forest interiors, where they foraged on red tree voles and northern flying squirrels. Timber harvest activities, including thinning of dense plantations, reduce the abundance of northern flying squirrels and red tree voles for several decades, contributing to a reduction in use by spotted owls (Carey 2000, Dunk and Hawley 2009, Gomez and Anthony 1998, Manning et al. 2012, Price et al. 2015, Waters and Zabel 1995, Wilson and Forsman 2013).

Disturbance

In this section, we define disturbances as modifiers of the structural characteristics, species composition, and landscape patterns of forest cover types used by spotted owls. The range of the northern spotted owl encompasses a variety of historical disturbance regimes that are fundamental to the health and diversity of these ecosystems (chapter 3). Important forest disturbances result from wildfire, forest management (e.g., thinning), timber harvests, extreme weather events, or forest insect and disease processes (Davis et al. 2016). Effects that forest disturbances have on spotted owls depends on spatial scale, severity, and season (McKelvey 2015). Biogeographic variation across the large range of spotted owls also results in very different levels of disturbance type, frequency, and severity (see “Wildfire” below). Major disturbance events influence forest cover types that have been used by spotted owls for many decades, and have different effects depending on the magnitude of change and the time since disturbance. For example, in the short term, a disturbance that creates open canopy conditions could reduce value for spotted owl roosting, but have long-term benefits by

enhancing understory vegetation diversity and conditions for spotted owl prey. Further, disturbances can stimulate the development of large-tree, complex-structure stand conditions over time (Lehmkuhl et al. 2015). An important secondary effect of forest disturbances for spotted owls are changes in prey abundance or vulnerability. These effects can be positive by creating conditions that increase abundance or vulnerability for some prey species, or negative by removing critical forest structure required by primary prey populations (e.g., northern flying squirrel, red tree vole) (Manning et al. 2012, Wilson and Forsman 2013). Some disturbances have a neutral affect, particularly when limited in severity or spatial extent, and ample suitable forest remains available at core and home-range scales.

Spotted owls were listed as a threatened species under the Endangered Species Act largely because of concerns regarding loss of old forest resulting from commercial timber harvest (Thomas et al. 2006, USFWS 2011b). Subsequent to reductions in harvest of old forest, high-severity wildfire has become the leading cause of suitable forest loss for spotted owls on federal lands, especially in fire-prone landscapes. However, commercial timber harvest still contributes substantially to the loss of suitable forest cover in some areas, especially on nonfederal lands (Davis et al. 2016, Pierce et al. 2005). Recent research on disturbance effects on spotted owls indicates that disturbances such as mixed-severity fires that generate heterogeneity at landscape and stand scales are not necessarily adverse, provided that adequate nesting and roosting structural conditions remain after the disturbance (Clark et al. 2013, Comfort et al. 2016). High-severity disturbances that broadly alter stands and landscapes within nesting territories can remove critical components of forest structure (e.g., high canopy cover and density of large live trees) required for spotted owl survival and reproduction (Dugger et al. 2005, Franklin et al. 2000, Olson et al. 2004). Timber harvesting and wildfire can both reduce the living tree components of a stand and reduce the overall suitability for spotted owls (see sidebars on pages 265 and 266). An important difference between timber harvest and wildfire is the removal of trees and ground disturbance in a timber harvest. For most wildfires, there is limited physical soil disturbance (although fire



The graph to the right is from Davis et al. (2015) and shows the relationship between these classes and monitoring trends in burn severity classes.

Effects of Forest Disturbances on Nesting/Roosting Forest Cover

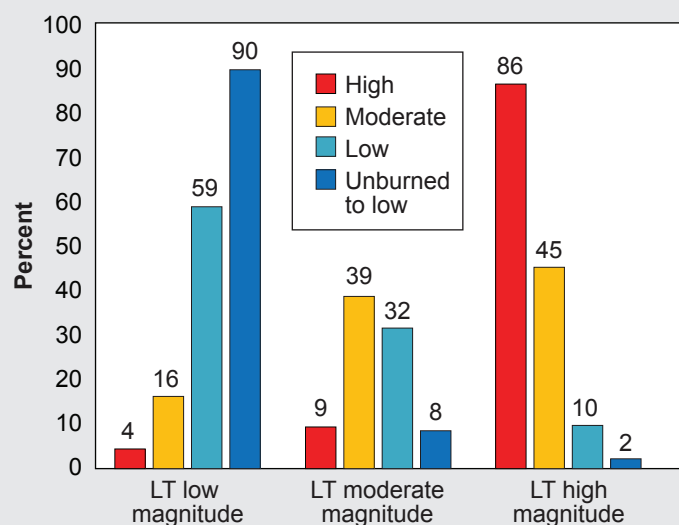
Map data from the most recent northern spotted owl habitat monitoring report (Davis et al. 2016) and Forest Inventory Analysis and Current Vegetation Survey plots were used to assess changes resulting from forest disturbances on stand structure elements used in the Davis et al. (2011, 2016) nesting/roosting cover type modeling and mapping procedure.

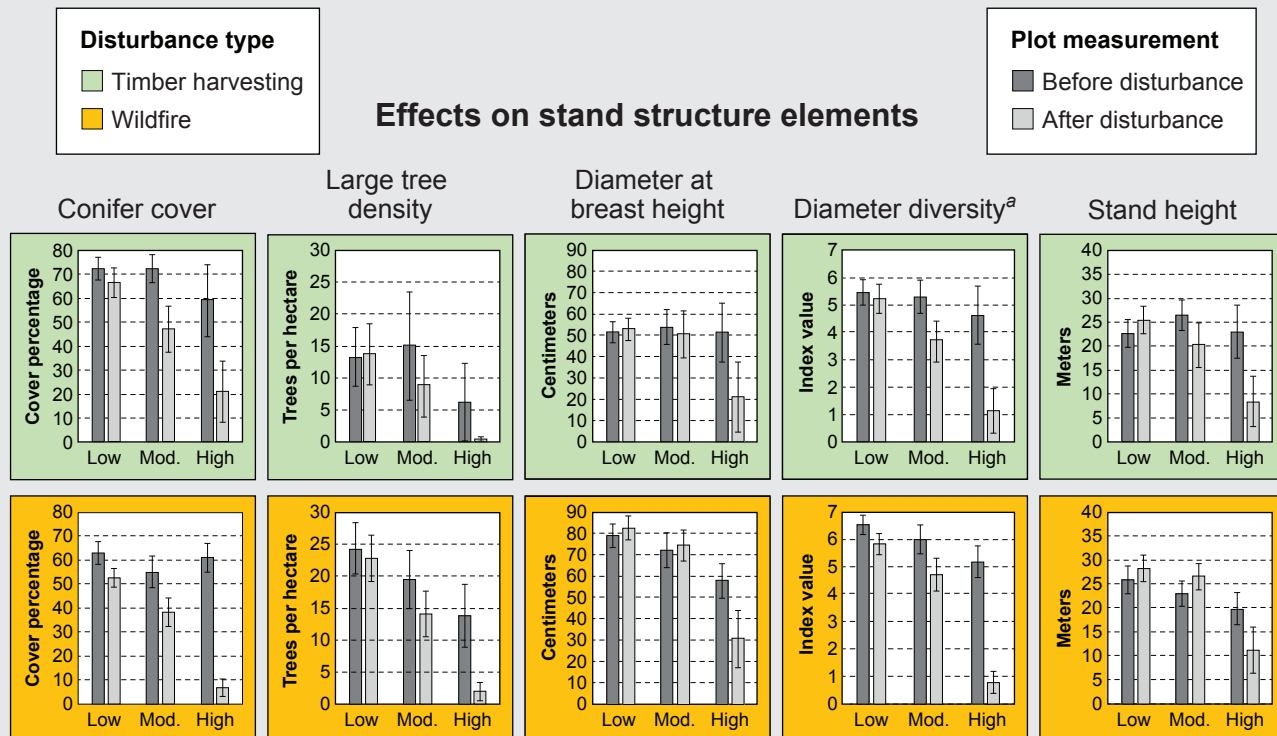
Plots used in this analysis occurred in mapped suitable nesting/roosting cover type in 1993 that experienced a disturbance between 1994 and 2012 from either timber harvesting or wildfire, which occurred between the initial plot measurement and re-measurement dates.

Changes in the mapped nesting/roosting relative suitability index were also analyzed by differencing the 2012 and 1993 relative suitability maps.

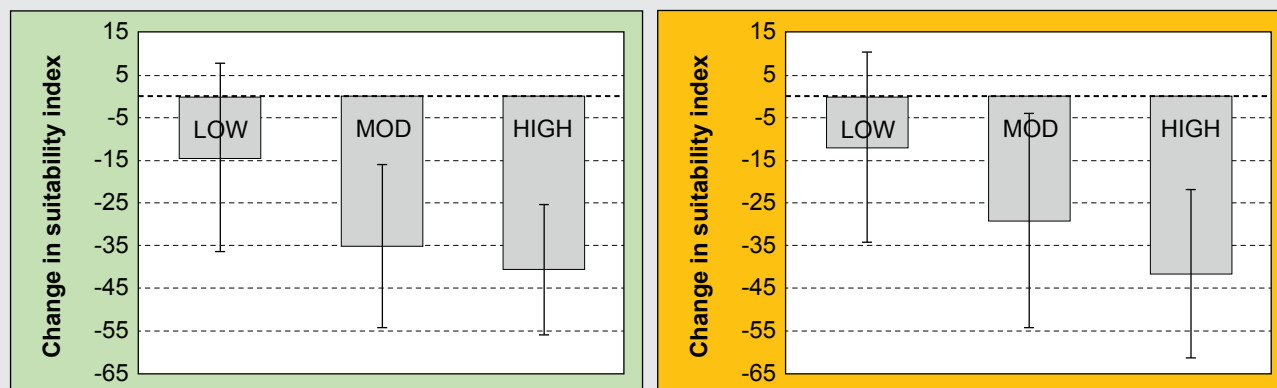
LandTrendr (LT) data (Kennedy et al. 2012) of forest disturbance magnitude are satellite-based measurements of loss of vegetation cover. We divided them into three classes:

- Low (<33 percent cover loss)
- Moderate (33 to 66 percent cover loss)
- High (>66 percent cover loss)





Effects on modeled relative suitability^b of forest cover types used for nesting and roosting



^a The diameter diversity index is a measure of the structural diversity of a forest stand based on live tree densities in diameter at breast height classes. An index value of 1 represents a single-story stand. Higher index values represent more complex multistoried stand structure.

^b Modeled relative suitability from Davis et al. (2016). The index for suitable nesting/roosting forest cover type ranges from 31 to 40, depending on the modeling region.

can have substantial impacts on soil chemistry and organic matter composition), and patches of live trees, snags, and logs remain in situ, which contributes to enhanced biodiversity, future quality of complex forest, and forest succession (Swanson et al. 2011).

Wildfire—

Wildfires occur throughout the entire range of the spotted owl. Some physiographic provinces are more environmentally suitable for wildfire occurrence at a decadal scale, while other provinces have wildfire-return intervals of several centuries (see chapter 3) (Agee 1993). Beyond frequency, the severity and spatial extent of wildfires differ across the NWFP area (Davis et al. 2011). The physiographic provinces of the eastern Cascades, southern portions of the western Cascades, and the Klamath Mountains are characterized by frequent low- and mixed-severity fire regimes (Baker 2015, Hessburg et al. 2007, Perry et al. 2011). Owing to more than a century of fire exclusion (e.g., from grazing, fire suppression, and historical forest management practices), many of these fire-prone landscapes have experienced significant increases in stand density and loss of large trees, threatening forest health and biodiversity (Hagmann et al. 2013, 2014; Hessburg et al. 2007; Perry et al. 2011). The historical extent of forest cover types suitable for nesting and roosting by spotted owls in dry and mesic mixed-conifer forests in the eastern Cascades and other fire-frequent forests was likely historically limited but has increased substantially in recent decades (Hagmann et al. 2013, 2014; Hessburg et al. 2007; Merschel et al. 2014). Moreover, in this fire-prone landscape, forest structure conditions that are more resilient to low- and mixed-severity fires (i.e., single-story old forests with large ponderosa pines) are not suitable for nesting and roosting by spotted owls. Areas occupied by spotted owls in the fire-prone landscapes of the eastern Cascade Range are often dense, closed-canopy, medium-size tree forests with a substantial true fir (*Abies* spp.) component and structural diversity enhanced by a variety of insect and disease processes, including dwarf mistletoe (Stine et al. 2014). These are the conditions that have been promoted through fire suppression and removal of fire-resilient large Douglas-fir and ponderosa pine trees. Compared to forest structure

conditions that are more resilient to wildfire, areas occupied by spotted owls in these fire-prone landscapes are at higher risk to high-severity wildfire (Dennison et al. 2014, Stine et al. 2014). All forest types in these landscapes are vulnerable to substantial impacts from high-severity wildfire under extreme weather conditions, which are likely to be more common with climate change (Kennedy and Wimberly 2009, Reilly et al. 2017).

West of these fire-prone areas to the Pacific coastline, the forests become progressively moister and less prone to frequent large wildfire. In these moist forests, large wildfires tend to be infrequent to moderately frequent, and fire severity trends from mixed to high severity (see chapter 3). In less fire-prone landscapes, old and complex forest with large trees—compared to other forest types—has higher moisture retention and cooler microclimates compared to other forest types, and may enhance biodiversity under a changing climate (Frey et al. 2016). In these mixed- and low-frequency fire regime landscapes, old forest may be more resistant to wildfire than young forest with closed canopy under normal fire weather conditions (Thompson and Spies 2009).

Throughout the NWFP area, the fundamental association between spotted owls and multilayer forests with large trees and closed canopies is well established (Dugger et al. 2016, Forsman et al. 1984, Franklin et al. 2000, Olson et al. 2005, Wiens et al. 2014). The severity of the wildfire has a strong influence on the degree to which these forest cover types are altered by wildfire (see sidebar on page 265). Low-severity wildfire can have very little effect on the suitability of nesting and roosting cover types, and can even increase it. Moderate-severity wildfire can change stand structure and species composition, resulting in moderate decreases in cover-type suitability. High-severity wildfire can alter forest cover to the point at which the area is no longer be suitable for nesting, roosting, or dispersal. Multiple lines of research have confirmed the effects of wildfire on stand structure and composition, but much less is understood about the short- and long-term response of spotted owls to wildfire.

Most studies focused on wildfire effects evaluated the short-term response of spotted owls to wildfire, but in one of the few studies of the long-term effects of wildfire

on spotted owls Rockweit et al. (2017) used 26 years of demographic data in a landscape with several wildfires and found that moderate and high burn severities negatively affected spotted owl apparent survival. They also found that burned territories functioned as ecological sinks where recruitment was high, but survival was lower than in nearby unburned territories. Several shorter post-wildfire studies have seemingly contradictory results regarding spotted owls and wildfire. For example, in an occupancy analysis, Jones et al. (2016) found high site extirpation rates of California spotted owls following a large, high-severity wildfire, but in a telemetry study, Bond et al. (2016) observed that burned forests were generally used in proportion to their availability. Other studies of California spotted owls and Mexican spotted owls have shown that wildfire does not necessarily decrease short-term occupancy in low- or moderate-severity burned areas (Bond et al. 2009, Ganey et al. 2011, Lee and Bond 2015, Lee et al. 2013, Roberts et al. 2011). Spotted owls can persist, at least for short periods, in landscapes that have experienced recent wildfires, as long as adequate moderate to closed-canopy nesting/roosting forest cover is retained at nesting core and home range scales. Even with high-severity wildfire, the effects can be insignificant or positive (e.g., increase vulnerability of prey) at larger spatial scales, especially if the forest cover changes caused by high-severity fire comprise only a small portion of a spotted owl's territory (Comfort et al. 2016).

Effects of wildfire interact in complex ways with other historic and current disturbances. Clark et al. (2013) found that local spotted owl site extinction probability was higher for sites with more combined area of past timber harvest, high-severity fire, and salvage logging. They also found evidence that colonization and occupancy rates were higher for sites with older forest burned at low severity (Clark et al. 2013). Coupling wildfire and salvage logging results in a high probability that a site becomes unoccupied after the first year postfire, especially if the core area burns at high severity and is subsequently logged (Bond 2016, Ganey et al. 2011, Lee et al. 2013). Beyond the effects on spotted owls, a human disturbance that directly follows a high-severity natural disturbance can have significant negative consequences to a forest ecosystem

by disrupting abiotic and biotic processes, reducing or eliminating biological legacies, simplifying post-disturbance structural complexity, altering vegetation recovery, diminishing natural patterns of landscape heterogeneity, facilitating invasion of nonnative species, decreasing native biodiversity, increasing susceptibility to erosion and repeated high-severity disturbances, and eliminating restorative benefits of disturbance events (Lindenmayer and Noss 2006, Thorn et al. 2017).

Overall, studies suggest that spotted owls are adapted to a forest landscape with a mosaic of successional stages shaped by historical disturbance regimes, accompanied by abundant prey resources, few barred owls, and structurally diverse closed-canopy forest with diffuse late-seral edge at the territory scale, and limited fragmentation occur within nesting areas (Dugger et al. 2011, Forsman et al. 1984, Franklin et al. 2000, Olson et al. 2004, Sovern et al. 2014). Research supports the premise that some spatial heterogeneity in forest conditions can have a positive effect on demography of spotted owls. At the territory scale (~500 to 1500 ha), a mosaic of older forest interspersed with other vegetation types, including early-seral and riparian forests, can promote high survival and reproduction of spotted owls (Comfort et al. 2016, Franklin and Gutiérrez 2002, Franklin et al. 2000). In terms of the effects of wildfire on spotted owls, we emphasize that most available research on impacts to spotted owls has been based to some degree on short-term responses and primarily focused on the other two spotted owl subspecies. The long-term (>5 years) effects of wildfire on spotted owl survival, reproduction, recruitment, and interactions with barred owls are not well documented.

Forest restoration and silvicultural treatments—

To meet management objectives of the NWFP, the spotted owl recovery plan, and critical habitat requirements, researchers and federal land managers have focused on ecosystem function (e.g., fire as an ecological process) in developing silvicultural practices that provide ecologically sustainable alternatives to clearcutting and old-growth harvest while still providing for timber production (chapter 3). As a result, alternative thinning methods, including variable-density thinning, have replaced clearcutting as the predominant form of active management on federal

lands, whether for restoration or timber production goals or both (Anderson and Ronnenberg 2013, Lehmkuhl et al. 2015). Ecological objectives for forest management differ by region, forest type, and historic disturbance regime (Franklin and Johnson 2012) (chapter 3).

Moist forest—The focus of silvicultural treatments in moist forests of the western Cascades and Coast Ranges (historically infrequent, high-severity fire regimes) has been an attempt to accelerate development of old-forest conditions in plantations or younger closed-canopy stands (Anderson and Ronnenberg 2013). Typical thinning treatments that create canopy gaps in moist forests west of the Cascade crest can create relatively rapid increases in understory vegetation diversity and productivity (Johnson and Franklin 2013) (chapter 3). The intensity and pattern of retained trees in forest thinning can have dramatic influence on microclimate and ecological response in the short term (Aubry et al. 2009, Heithecker and Halpern 2006). Stand conditions can be either too open or too dense for foraging because spotted owls are adapted to old forest with closed canopies, and the understory must be open enough to fly and access prey (Irwin et al. 2015). In areas where dusky-footed woodrats are primary prey (e.g., southern Oregon, northern California), thinning of young dense stands may increase spotted owl use for foraging, but still not create preferred forest conditions for other life history needs such as nesting and roosting (Irwin et al. 2015). Wilson and Forsman (2013) found that the abundance of mice, terrestrial voles, and shrews increased immediately following thinning, but that northern flying squirrels and red tree voles—important prey species for spotted owls—decreased dramatically in abundance in treated areas for up to 11 years after treatment (Wilson 2010). Thus, spotted owls respond to silvicultural treatments differently where the primary prey are northern flying squirrels, which includes most of the northern and western portions of their range in Oregon, Washington, and British Columbia.

When assessing the potential effects of thinning on prey species, the landscape context should be considered. For example, the effects of thinning within heterogeneous landscapes with well-connected, intact old-forest cover may be less detrimental to northern flying squirrels than if thinning occurs within a highly fragmented forest land-

scape (Sollmann et al. 2016). Some degree of landscape heterogeneity resulting from forest restoration activities in west-side forests does not adversely impact spotted owls, provided that sufficient large-tree, closed-canopy forest for nesting and roosting is available at core and home range scales (Andrews et al. 2005). For example, in northern California, Franklin et al. (2000) found that territories with the highest fitness (survival and reproduction) were those with a mixture of old forest and about 40 percent of other vegetation types. Diller et al. (2012) reported that forest cover heterogeneity (i.e., juxtaposition of young and older stands) had positive effects on survival and reproduction of spotted owls on commercial timberlands in northern California, where disturbance regimes were historically of mixed severity. Highly productive growing conditions and abundant hardwoods contribute to structural complexity in these managed forests. However, survival of spotted owls decreased in southern Oregon when the amount of nesting/roosting forest cover within the territory center was less than 50 percent (Dugger et al. 2005), and a similar relationship was found in other studies (Franklin et al. 2000, Olson et al. 2004, Wiens et al. 2014).

Dry forest—In the drier forests of the eastern Cascades, southern Oregon, and northern California, wildfire was historically more frequent and burned with mixed- and low-severity effects. In these areas, forest management treatments have focused on accelerating the development of old-forest conditions, but also have focused more on restoring or promoting fire-resilient forest structure, species composition, and landscape pattern (Hessburg et al. 2016, Lehmkuhl et al. 2015, Stine et al. 2014). Landscape managers implementing forest restoration treatments in drier, mixed- and low-severity fire regime forests face substantial challenges in balancing the tradeoffs between known short-term forest cover impacts on spotted owls from restoration and fuel reduction treatments versus potential benefits of reducing losses of forests with larger trees from high-severity, large-scale wildfire (Hessburg et al. 2015, 2016; Lehmkuhl et al. 2015; Stine et al. 2014). Management emphasis on wildfire suppression combined with historical harvest of large trees in these landscapes over the past 100 years has contributed to the recruitment of small-tree, closed-canopy forest

(Hessburg et al. 2016). In these regions, the moderate- to closed-canopy forest with multilayer canopy structure enhanced by dwarf mistletoe infestations are used by spotted owls for nesting and roosting areas, and appear to have increased over the latter part of the 20th century into the 21st century (Davis et al. 2016, Lint 2005). Large tree, multi-story canopy typical of forest cover types used for nesting and roosting by spotted owls across their range make them less flammable under most fire conditions, but, like most cover types, these are susceptible to burning intensely in extreme weather. Standard treatments focused on increasing stand-level resilience to wildfire by using prescribed fire and removing ladder fuels (e.g., Cochrane et al. 2012, Safford et al. 2012, Stephens et al. 2009), and reducing canopy connectivity (Agee and Skinner 2005) can reduce the risk of stand-replacement high-severity wildfires, but the practices also remove important forest cover elements for spotted owls and their prey (Lehmkuhl et al. 2006a, 2006b, 2015). Prescribed fire treatments as part of fuel reduction projects can further reduce under- and mid-story canopy complexity, and burn up logs and snags, potentially causing additional negative impacts to suitable forest for spotted owls and their prey (Lehmkuhl et al. 2015). Silvicultural practices that promote spatial and structural complexity have been proposed for retaining suitable foraging conditions for spotted owls while also reducing fuel loads (Churchill et al. 2013, Gaines et al. 2010, Hessburg et al. 2016, Johnson and Franklin 2013, Lehmkuhl et al. 2015). However, the effectiveness of these management practices to restore ecological resilience and reduce risk of loss to high-severity wildfire, while maintaining components of suitable forest for spotted owls, remains to be tested in dry forest landscapes (see chapters 3 and 12 for more discussion of this issue).

Several simulation studies have used coupled wildfire and forest growth models to investigate the relative effects of wildfire and forest restoration treatments on recruitment and retention of forest cover types used by spotted owls in fire-prone landscapes. Some of these studies suggest that certain fuel treatment scenarios (i.e., active management) can reduce wildfire-caused losses of forest cover types used by spotted owls (Ager et al. 2007, Roloff et al. 2012). Other

modeling efforts found that active management reduced forest cover used by spotted owls more than simulations with no management, (Roloff et al. 2005, Spies et al. 2017). As with any modeling exercise, outcomes of these studies reflect the assumptions incorporated into the simulations. Assumptions regarding wildfire severity, return intervals, and effects of treatments are particularly influential. One general theme from these simulations is that benefits of fuel treatments to forest types used by spotted owls depend on what probability of occurrence is assumed for future high-severity wildfires. If the likelihood and impacts of high-severity wildfire are assumed to be high, thinning treatments are more likely to have a positive outcome for spotted owls (e.g., Roloff et al. 2012). If the likelihood of high-severity wildfire is assumed to be low, however, then thinning treatments are more likely to produce only declines in the amount of suitable forest cover types used by spotted owls.

Climate Change

Climate change will affect spotted owl populations through changes in weather, forest cover, disturbance processes, prey availability, and other ecological interactions. Population growth of spotted owls appears to be positively associated with wetter than normal conditions during the growing season (May–October), which likely increases prey populations and thus availability (Glenn et al. 2010). Population growth and reproduction were also negatively associated with cold, wet winters (pre-nesting) and the number of hot summer days (July–August) (Diller et al. 2012, Glenn et al. 2011b). Annual survival was more closely related to regional climate conditions (Southern Oscillation Index [SOI] and Pacific Decadal Oscillation [PDO]), whereas recruitment was often associated with local weather. Projected future climate conditions have the potential to negatively affect annual survival, recruitment, and, consequently, population growth rates for spotted owls (Glenn et al. 2010). Climatic factors affecting vegetation and prey abundance likely have a greater effect on reproduction and population growth than direct effects of weather on nestlings or adult spotted owls (Glenn et al. 2011a, 2011b). Climate change models for the first half of the 21st century predict warmer, wetter winters

and hotter, drier summers for the Pacific Northwest (Mote et al. 2003) (chapter 2). These conditions are expected to decrease survival of spotted owls in some areas (Glenn et al. 2011a). Climate change can affect development of forest structure by altering temperature and precipitation regimes, and disturbance frequency and intensity (Dale et al. 2001). Altered understory vegetation can reduce prey availability and thus spotted owl fitness (Carey and Johnson 1995, Franklin et al. 2000). Carroll (2010) found that vegetation rather than climate variables best explained distributions of spotted owls. Potential climate-related forest cover losses resulting from large-scale, high-severity wildfires and increased mortality of old-growth trees (Van Mantgem et al. 2009) may be particularly important for future viability of spotted owl populations (chapter 2).

Franklin et al. (2000) found that forest cover patterns explained a high amount of spatial variation in fitness potential among territories occupied by spotted owls in northern California, but climate explained most of the temporal, year-to-year variation in fitness-related traits. Survival and reproduction, for example, were lower when the early nesting period (February–March) was cold and wet. Fecundity, recruitment, and survival decreased across the range of the spotted owl when winters or early springs were colder and wetter than average (Diller et al. 2012; Dugger et al. 2005, 2016; Forsman et al. 1984, 2011). Spotted owl populations in drier forests may be especially vulnerable to climate change because hot, dry summers can reduce prey abundance or availability, and subsequently reduce spotted owl survival (Glenn et al. 2011a). Regional climate patterns, including the SOI and PDO, have also been correlated with demographic rates of spotted owls (Dugger et al. 2016; Forsman et al. 2011; Glenn et al. 2010, 2011a, 2011b). Survival of spotted owls was greater when the PDO was in a warming phase and lower when the SOI was negative (i.e., El Niño events resulting in higher than average temperatures and below normal precipitation) (Dugger et al. 2016).

Extrapolation of the best combination of vegetation-climate models to predicted future climates suggests northward expansion of high-suitability forest cover for spotted owls (Carroll 2010). Increased winter temperature under future climates might be expected to increase winter

survival and nesting success, and allow range expansion of prey species such as woodrats, which currently occur at high densities only in the southern portions of the range (Noon and Blakesley 2006). However, it is uncertain how barred owls will respond to changing prey populations, and model results suggest that an initial expansion in the suitable climatic niche may be followed by a contraction as climate change intensifies (Carroll 2010). An important qualifier is that these models did not account for losses of multilayered forests to wildfire and the potential for competition with barred owls to become even more prevalent as climatic change causes shifts in forest communities that in turn further constrain both owl species to a common set of increasingly limited resources.

Other Threats

Genetic diversity and hybridization—

Loss of genetic diversity within a population can contribute to inbreeding depression and decrease adaptive potential. Increased rates of hybridization with barred owls may further compromise the genetic integrity of the spotted owl population (Funk et al. 2010, Gutiérrez et al. 2007). Genetic studies have reinforced other studies that showed spotted owl population declines. Specifically, genetic evidence indicates a loss of genetic variation and increased potential for inbreeding depression in small populations. This suggests a vulnerability of spotted owls to extinction (Funk et al. 2010). Genetic data from spotted owls have indicated population bottlenecks for the Washington eastern Cascades, northern Oregon Coast Range, and Klamath Mountains (Funk et al. 2010), which corresponded temporally with population declines in most of those regions (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011). There was, however, no definitive evidence that suitable forest cover associated with dispersal was limited, or that gene flow was restricted in those regions (Barrowclough et al. 2005, Davis et al. 2011).

Hybridization with barred owls is another potential threat to spotted owl persistence, especially as the spotted owl becomes increasingly rare and the invading species becomes more abundant (Gutiérrez et al. 2007, Haig et al. 2004). Spotted owls occasionally mate with barred

owls (male spotted owl–female barred owl mating is most common) and produce fertile hybrids (Hamer et al. 1994, Kelly and Forsman 2004). In the southern portion of the spotted owl range, 3 percent of spotted owl genetic samples collected prior to 2004 (barred owls were still relatively rare on the landscape) contained barred owl mitochondrial DNA (Barrowclough et al. 2005). There are typical markings of hybrids that can be helpful in field identification (Hamer et al. 1994), but genotyping potential hybrids across generations has shown that field identifications were often wrong (Funk et al. 2007). Hybridization rates may also have changed substantially in recent years as barred owl populations have increased and spotted owls have decreased.

Hybridization with other spotted owl subspecies does not appear to be a concern for spotted owl conservation. The northern spotted owl and California spotted owl are two well-differentiated subspecies connected by a narrow hybrid zone in a region of low population density for both subspecies in north-central California (Barrowclough et al. 2005, 2011; Funk et al. 2008; Gutiérrez and Barrowclough 2005). Spotted owls in the contact zone are highly differentiated and may be a distinct population from other northern spotted owl and California spotted owl populations (Miller et al. 2017).

Diseases and pathogens—

Disease exposure could be a secondary consequence of climate change, blood parasites, and effects of barred owl interactions. Lewicki et al. (2015) found that spotted owls had a higher *Haemoproteus* spp. parasite diversity and probability of infection than sympatric barred owls. Further, avian malaria (*Plasmodium* spp.) is common in barred owls, and only recently was documented in spotted owls; therefore, barred owls likely have an additional competitive advantage because spotted owls are potentially immune-compromised owing to recent exposure to avian malaria (Ishak et al. 2008). Spotted owls are susceptible to West Nile virus and experience high rates of mortality when exposed (Courtney et al. 2004); however, it is unknown what, if any, population-level impacts the disease has caused. Wiens et al. (2014) reported that the leading cause of death in a sample of radio-marked barred owls was bacterial infection associated with endoparasitism.

Environmental contaminants—

Environmental contaminants, especially anticoagulant rodenticides, have recently emerged as a potential threat to spotted owls and their prey. In particular, anticoagulant rodenticides used in illegal marijuana cultivation and urban settings can have significant indirect impacts by the poisoning of nontarget forest predators, including owls (Albert et al. 2010, Gabriel et al. 2012, Riley et al. 2007, Stone et al. 1999). To our knowledge, no studies have addressed potential effects of anticoagulant rodenticides on spotted owls.

Research Needs, Uncertainties, Information Gaps, and Limitations

Research Needs

Effects of barred owls—

It has become increasingly clear that barred owls are a primary driver of spotted owl population declines, but many questions remain about the full impact of barred owls directly on spotted owls, and indirectly through alterations of forest communities. Research is needed to build on the work of Wiens et al. (2014) and others to identify potential processes by which spotted owls and barred owls use resources differently. More research is needed to establish the full suite of cause-and-effect relations of barred owl impacts on spotted owls, and how barred owls interact with other threats to spotted owls. Unfortunately, these types of studies are becoming increasingly difficult because spotted owl numbers are declining so rapidly on most study areas. In a pilot study, Diller et al. (2016) found that spotted owls responded positively to experimental removal of barred owls, but additional removal studies in other physiographic provinces, where owl populations and suitable forests are different, are needed. To determine the feasibility and effectiveness of barred owl removals as a tool for spotted owl recovery, the Fish and Wildlife Service and U.S. Geological Survey initiated a barred owl removal experiment on four study areas in Washington, Oregon, and northern California (USFWS 2013). Continued monitoring of spotted owl populations in those areas will be required to fully assess the short- and perhaps, in particular, long-term response of spotted owls to the removal of an important competitor. More genetic studies are needed to address the frequency

and impact of hybridization between spotted owls and barred owls, and how hybridization rates may have changed with changes in abundance of the two species.

It remains uncertain how climate change will affect interactions between spotted owls and barred owls, or even where barred owl populations are in terms of the invasion process. For example, little research has been conducted to investigate if populations of barred owls are continuing to increase or if carrying capacity has been met in some regions. Fundamental information on barred owl distribution and population trends is needed to address this important issue. Further, little is known about barred owl distribution and populations beyond forest cover types occupied by spotted owls. Ecologists are being challenged to predict how spotted owls will change in abundance and distribution under current climate, availability of suitable forest, and competitive interactions with barred owls. It is well documented that climate change influences species' abundances and distributions, and can have indirect effects on interspecific interactions (Angert et al. 2013). An important area of needed research related to barred owl-spotted owl interactions and climate change will be to better understand how the combined effects of barred owl competition and future changes in the amount and distribution of forests used by spotted owls might contribute to spotted owl population persistence and range shifts under a changing climate.

In addition to impacts on spotted owls, changes in the abundance and distribution of a generalist apex predator like the barred owl can have cascading effects on prey populations and food-web dynamics (Gutiérrez et al. 2007, Holm et al. 2016, Wiens et al. 2014). Barred owls have reached densities in the Pacific Northwest that are far greater than historical populations of northern spotted owls (Wiens et al. 2011, 2014). Moreover, as generalist predators, barred owls capture a greater proportion of diurnal, terrestrial, and aquatic prey than northern spotted owls (Forsman et al. 2004, Hamer et al. 2001, Wiens et al. 2014). These life-history traits indicate that barred owls are not direct functional replacements of northern spotted owls in forested ecosystems of the Pacific Northwest (Holm et al. 2016), and that a wide range of prey species may be affected if they

replace northern spotted owls. Further research is needed to determine the potential effects of barred owls on other sensitive wildlife beyond spotted owls.

Finally, critical needs for managers are detailed assessments of those locations where spotted owls persist and a better understanding of the effects of forest management activities on interactions between spotted owls and barred owls, and the species individually. Many spotted owl sites with apparently suitable forest structure for nesting and roosting have been abandoned as a result of displacement by barred owls. Those sites that spotted owls have persisted in the face of barred owls may be a result of the behavioral characteristics of the territorial spotted owl, or perhaps those sites have unique forest characteristics that enhance coexistence between the two species. Thinning treatments could potentially affect competitive interactions either by displacing barred owls into areas occupied by spotted owls, or potentially increasing foraging opportunities for barred owls over spotted owls. These and many other responses are plausible, but it remains unknown how either species responds to many forest management techniques. Recent advances in lightweight geographic positioning system telemetry devices and high-resolution forest structure mapping technologies can provide new opportunities for advancing our understanding of these issues.

Prey populations and population performance—

Previous studies have characterized the diet of spotted owls in different portions of the subspecies' range (Barrows 1980; Bevis et al. 1997; Cutler and Hays 1991; Forsman et al. 1984, 2001, 2004), investigated the relationship between forest cover selection, home-range size, and prey availability (Carey et al. 1992; Forsman et al. 1984, 2005; Irwin et al. 2000; Zabel et al. 1995), and evaluated diet overlap with barred owls (Hamer et al. 2001, Wiens et al. 2014). The importance of understanding relationships between spotted owl populations and their prey has repeatedly been acknowledged (Clark et al. 2011, Courtney et al. 2004, Forsman et al. 2004, Glenn et al. 2010, Olson et al. 2004, Rosenberg et al. 2003, Thomas et al. 1990, Wilson and Forsman 2013, Zabel et al. 1995). However, to our knowledge, no efforts have been undertaken to quantify the relationship between interannual fluctuations in prey abundance and

long-term demography of spotted owls. Research is needed to understand how spotted owl reproduction, stress levels, and survival are influenced by prey species composition and abundance, and how prey populations are influenced by disturbance or fluctuations in weather and climate. Population fluctuations in small mammals have been linked with variation in precipitation (Avery et al. 2005, Crespin et al. 2002). However, identifying the mechanisms by which climate influences population processes of spotted owls and their prey remains a challenge (Glenn et al. 2011a).

A better understanding of the effects of thinning treatments and the impacts that anticoagulant rodenticides have on spotted owl prey populations will be critical for managers. Research and an effect analysis is needed to address thinning impacts on spotted owl prey, both within treated stands and at broader landscape scales. This information would contribute to thinning prescription development throughout the range of the spotted owl. The use of anticoagulant rodenticides in natural systems is increasing, especially in areas where illegal marijuana cultivation is prevalent. Studies are also needed to better understand the individual- and population-level impact of rodenticides on spotted owls, and development of management options to reduce the ecological impacts.

Landscape restoration, silvicultural treatments, prescribed fire, and wildfire in moist and dry forests—

Research is needed in both dry and moist forest landscapes to evaluate the short- and long-term effects of silvicultural treatments and wildfire on spotted owl occupancy, forest dynamics, and prey, but research questions differ between forest types. For example, the optimization of forest restoration and conservation of spotted owls will require more knowledge about the conditions under which restoration activities can benefit spotted owls in the long term without significant detrimental impact in the short term. Restoration activities and objectives are different between moist and dry forest landscapes. Current conditions in dry forests are generally not sustainable, and some measure of treatment is needed to increase fire resiliency of forest stands in at least some locations (USFWS 2012b). In these fire-prone landscapes, a common objective is to modify and reduce fuels to alter wildfire behavior and to manage for ecological integrity

based on the natural range of variability (USDA 2012). Additional information is needed to evaluate the consequences of fuels reduction and restoration treatments relative to the long-term benefits of forest restoration, particularly as large, high-severity fires are expected to become more frequent because of climate change. This is especially true in the frequent low-severity fire regime of the eastern Cascades, where environmental conditions favor open pine-dominated forests. Studies are needed to identify resilient sites for spotted owls in the face of changing forests (e.g., species composition changes) caused by climate change, active forest management, and increased wildfire occurrence.

In moist forest landscapes, research is needed to determine how or if spotted owls use forest stands where thinning has been conducted to accelerate the development of late-successional forest characteristics. If spotted owls avoid these areas in the short term, work is needed to understand the time before they begin using the areas again. To fully understand restoration effects, long-term before/after control-impact studies are needed to elucidate spotted owl and prey responses to forest restoration treatment effects in different ecotypes.

Research to address restoration and silvicultural treatment on spotted owl space use and forest structure development will also need to account for the potential confounding impact that barred owls are likely to have on spotted owl response to restoration efforts. Beyond a better understanding of spotted owl response to silvicultural treatments, managers need information regarding how sympatric populations of barred owls respond to treatments. Additionally, research is needed to understand the effectiveness of ecosystem-scale conservation versus conservation that targets one particular stage of succession (e.g., late-successional forest characteristics for spotted owls). Finally, much more information is needed to evaluate the short- to long-term effects that wildfire has on spotted owls in all landscapes, with a focus on the relative susceptibility of old forest and young forest to high-severity wildfire under a range of weather conditions. Finally, it is important to note that these research topics become increasingly difficult to address as spotted owl populations decline and fewer individual owls are available to study in some landscapes.

Physiological consequences of stress—

An animal's ability to cope with stressors is an important determinant of its physiological conditions, and therefore, health and survival. Environmental perturbations and an individual's response can affect the body's production of hormones, such as glucocorticoids, with negative physiological consequences (Carrete et al. 2013, Strong et al. 2015). For many species, the level of stress hormone corticosterone can be an effective predictor of survival probabilities, reproduction, dispersal, and can have population-level impacts (Carrete et al. 2013, Romero and Wikelski 2001, Romero et al. 2000). Quantification of corticosterone in feathers, which is stable over time, represents an integrated measure of stress levels (Bortolotti et al. 2009, Sheriff et al. 2011). Stress hormones are accumulated in feathers during growth, so can provide a measure of stress levels during that time, and can be a strong predictor for future survival of individuals (Koren et al. 2012). Variation in feather corticosterone can also be quantified among individuals of a population, as well as through time to track stress over space and time to address questions about the health and ecology of a population (Bortolotti et al. 2009).

Hayward et al. (2011) found that spotted owls had a glucocorticoid response to acute noise disturbance and that spotted owls with nests near noisy roads fledged fewer young than those near quiet roads. Corticosterone analyses are needed to determine the physiological response to acute and prolonged exposure to environmental stressors (e.g., barred owls, prey abundance, weather, and human-caused disturbance) and response activity for both juvenile and adult spotted owls. Our understanding of spotted owl ecology will be improved with studies to evaluate the associations between stress levels and survival, reproduction, and dispersal of spotted owls. From a management perspective, it is important to understand the stress response of spotted owls related to management activities like prescribed fire, road construction, various logging systems, and the timing of these activities. Additional research will be important to understand key stressors for spotted owls and inform seasonal restrictions on human activities that can increase stress levels.

Dispersal and suitable forest connectivity—

Dispersal behavior for both juveniles and adults may increase survival and reproductive success, but also increase risks to establishing a home range in an unfamiliar landscape. Juvenile spotted owls disperse within their first year and the condition of matrix forest types between natal and breeding sites can facilitate or hamper survival and movement processes (Forsman et al. 2002). Available information for spotted owls suggests that stands used for roosting during natal dispersal movements have very similar structure as those stands used for nesting and roosting activities of adults (>70 percent canopy cover and large trees >50 cm d.b.h.), but this finding is based on only two studies with no data throughout most of the geographic range (Miller et al. 1997, Sovern et al. 2015). Further research is needed to understand the contemporary dynamics of juvenile dispersal because many assumptions are made about what constitutes forest cover suitable to facilitate dispersal by spotted owls. A better understanding of the forest structure and configuration characteristics of forest conditions that facilitate juvenile dispersal is needed to ensure demographic connectivity among isolated patches of remaining old forests. Further, it remains unknown how barred owls influence juvenile spotted owl survival or dispersal. It is possible that some of these questions could be addressed with a thorough analysis of existing dispersal data from demographic study areas.

Historically, adult spotted owls exhibited strong nesting-site and mate fidelity, with fewer than 8 percent of individuals dispersing to a different territory between years (Forsman et al. 1984, 2002). In recent years, however, field observations suggest that interterritory movements by resident spotted owls are increasing, and that such movements appear to coincide with the colonization of barred owls (Dugger et al. 2011, Olson et al. 2005). Research that addresses how forest alteration and the presence of barred owls interact with social conditions on territories to affect movement decisions and survival of individual spotted owls will improve our ability to implement forest management practices that benefit spotted owls. In addition to helping land managers identify the range of conditions within

individual owl territories that promote high site fidelity and survival, such data can also provide a powerful framework for testing broad ecological theories about the causes and consequences of breeding dispersal in a long-lived predatory bird with declining populations.

Testing alternative monitoring protocols—

When the NWFP was developed, mark-recapture and random census (i.e., occupancy framework; the proportion of sites occupied by spotted owls) population monitoring methods were both considered. The decision was made to use the mark-recapture method, which was already in use. Precise estimates from mark-recapture studies require large samples of marked spotted owls; therefore, Lint et al. (1999) recommended the use of an independent estimate of population trend for comparison with the results from spotted owl demographic studies. Monitoring in an occupancy framework (i.e., MacKenzie et al. 2006) could provide an independent, empirical assessment of population trends to compare with estimates of the annual rate of population change. Because of uncertainty about the precision of the occupancy-based approach, Lint et al. (1999) recommended that statistical power and cost effectiveness of the method be explored.

The low number of spotted owls in some study areas suggests that passive acoustic monitoring may be an effective solution for future monitoring of spotted owl populations. Traditional call-back surveys at night (playing spotted owl calls and listening for a spotted owl response) are labor intensive, more risky compared to daytime work, and only generate reliable data for spotted owls. Further, detection probabilities for spotted owls—using call-back surveys—are negatively influenced by the presence of barred owls, and barred owls often do not respond to spotted owl calls (Bailey et al. 2009). Call-back surveys could also have unintended consequences by exposing spotted owls to predation or harassment by barred owls or great-horned owls. Primary advantages of passive acoustic monitoring are as follows: (1) surveys do not require an elicited response from target species; (2) surveys are able to detect and do not bias against many

other species (e.g., barred owl, marbled murrelet, western screech-owl, northern pygmy-owl, northern saw-whet owl, and many others); (3) increased crew safety because all work would be conducted during daylight hours; (4) biological training and expertise needed for crew members will be much less than is needed for call-back surveys and demographic studies; and (5) sound recordings provide a permanent record of the detection. A limitation of this approach is the time required to process recordings and data storage. Automated call detection technology has been developed, but improvements are needed, especially for call recognizers for rare birds in areas with excessive background environmental noise (e.g., rain, streams). Research is needed to test alternative methods that take advantage of technological advancements in noninvasive detection equipment to monitor trends in rare populations. The transition to alternative methods to monitor spotted owl populations will be most effective if new methods have spatial and temporal overlap with traditional methods so that robust comparisons can be made between historical and contemporary data.

Population simulation modeling—

The program HexSim (Schumaker 2015) provides a simulation framework for systematically investigating factors that influence population function, including forest conservation scenarios and emergent competitors. The implementation of HexSim by the USFWS (2011b) did not include spatially explicit representation of spotted owl interactions with barred owls. Modeling exercises that incorporate a more sophisticated representation of population interactions with barred owls are needed to simulate and predict responses of spotted owls to experimental removal of barred owls. Two-species models implemented in HexSim could also be used to simulate potential efficacy of long-term management programs for barred owls and spotted owls relative to critical habitat designations. Current modeling efforts are female-only models. A two-sex HexSim implementation for the spotted owl population is needed to get at small population processes (e.g., Allee effects and stochasticity in sex ratios) that can drive extinction.

Scientific Uncertainty

Survival estimates—

Adult survival is typically the most important factor influencing population performance in long-lived raptors, and survival estimates for spotted owls have been the focus of extensive research and monitoring. As in other meta-analyses of spotted owl demographic data (e.g., Burnham et al. 1996, Dugger et al. 2016, Forsman et al. 2011), Anthony et al. (2006) used capture-recapture methods to estimate apparent survival rates of spotted owls. Apparent survival is the product of probabilities that an animal survives and remains in the population. If a marked animal permanently emigrates, then it is, for purposes of the estimate, presumed dead, because emigration and mortality are confounded. Further, fates are not known for all individuals because recapture probabilities are less than one even when animals remain in the population. Therefore, models based on capture-recapture data account for imperfect encounter rates in estimates of survival (i.e., apparent survival). Apparent survival rates on individual study areas ranged from 0.75 (± 0.03) to 0.89 (± 0.01) for adults, 0.63 (± 0.07) to 0.89 (± 0.01) for 2-year-olds, and 0.42 (± 0.11) to 0.86 (± 0.02) for 1-year-olds. They found negative effects of reproduction and barred owls in survival rates on several study areas (Anthony et al. 2006).

Elsewhere, Loehle et al. (2005) used telemetry to study annual survival of spotted owls and obtained a known-fate estimate of 0.93 (± 0.07), which was considerably higher than the apparent survival estimates reported by Anthony et al. (2006). Known-fate models estimate survival rate when fates (i.e., alive or dead) of individuals can be determined with certainty. Loehle et al. (2005) used their results to cast doubt on apparent survival estimates from mark-recapture studies of spotted owls. They suggested that survival estimates from mark-recapture studies were too low because some marked individuals left the study areas and were assumed to be dead. Anthony et al. (2006) estimated a declining spotted owl population; Loehle et al. (2005) suggested that the true population change for spotted owls was likely stable and not declining. In response, Franklin et al. (2006) argued that Loehle et al. (2005) had inappropriately compared their study with the work of Anthony et

al. (2006) in a number of ways, including (1) the manner in which missing radio-marked individuals were removed from analyses may have overestimated survival; (2) telemetry-based estimates of survival were not valid for estimating bias; and (3) results from the telemetry-based study should not be compared to the capture-recapture study because study areas differed dramatically in size and distribution. Both apparent survival estimates from mark-recapture data and known-fate estimates from telemetry studies are valid estimates of annual survival. However, in this circumstance it was inappropriate to compare telemetry-based survival estimates with results from capture-recapture studies, which was acknowledged by both sides of the disagreement (Franklin et al. 2006, Loehle and Irwin 2006).

Wildfire risk—

The 2008 recovery plan (now withdrawn) for spotted owls (USFWS 2008) suggested a change in the LSR network as the foundation of conservation strategies established in the NWFP. Because of concern about wildfire, the plan recommended a switch from a reserve to a no-reserve strategy in up to 52 percent of the spotted owl's range. For dry forests, the plan recommended thinning stands at regular intervals to reduce fuel loading, and thus wildfire risk. Hanson et al. (2009) suggested that the estimates of wildfire risk used by the USFWS (2008) were overestimated and that there was not a strong basis for major changes to the NWFP conservation strategy for the spotted owl. Spies et al. (2010) defended the estimates of wildfire risk and suggested that Hanson et al. (2009) had underestimated wildfire risk and were biased against active management. Hanson et al. (2010) then responded by calling for less focus on fuel treatments in the recovery plan for the spotted owl. Because of uncertainty about future wildfire occurrence, spatial extent, and severity, we cannot know with complete confidence whether wildfire risk has been over- or underestimated in these efforts. Both the 2008 critical habitat designation and the 2008 recovery plan were challenged in court, and the inspector general of the Department of the Interior issued a report concluding that the decisionmaking process for the

recovery plan was potentially jeopardized by improper political influence (Devaney 2008, USFWS 2011a). The court ordered the Fish and Wildlife Service to withdraw the 2008 recovery plan and issue a revised recovery plan and critical habitat designation.

Spies et al. (2017) projected that the extent of forest cover suitable for spotted owls in the eastern Oregon Cascades is expected to increase in coming decades under recent historical frequencies and severities of wildfire (and current levels of wildfire suppression). Treating the landscape to reduce potential loss of suitable forest cover for spotted owls with high-severity wildfire still resulted in increases in that forest cover type, but not as much as would occur without management. The results suggest that managing for resilience to fire and climate change could occur without necessarily reducing forest cover from its current levels (younger forest is growing into older closed-canopy forests to replace dense forests lost thinning or wildfire). However, these outcomes are likely to be different under climate change or if an alternative landscape-scale treatment design is used (Spies et al. 2017).

Despite the potential negative effects on spotted owl habitat, the overwhelming consensus in the scientific literature is that active management in dry forests is appropriate to reduce wildfire risk and improve ecosystem function. Therefore, the 2011 revised recovery plan (USFWS 2011b) and 2012 critical habitat designation (USFWS 2012a) for spotted owls contained proposals for active management in dry forests. In some regions, project planning has moved forward, and federal land managers are consulting with the Fish and Wildlife Service on a case-by-case basis. The debate about active management related to wildfire risk for forests used by spotted owls remains unresolved and reflects different goals (e.g., ecosystem versus single species) and assumptions about wildfire risk with a changing climate. These differences of opinion highlight legitimate concerns about where to place the burden of proof regarding ecosystem versus species management, but the fundamentals of this controversy lie in the diversity of philosophical views about ecological goals and the role that active management should play on public lands (see chapter 12).

Restoration framework—

Franklin and Johnson (2012) outlined a series of recommendations for an “ecological forestry” framework and a forest restoration strategy within the Plan area that reflect many of the elements of the revised spotted owl recovery plan (USFWS 2011b). They called for reserving older forest stands, thinning plantations to accelerate development of structural complexity, and implementing variable-retention harvests in younger forests to help provide diverse early-seral ecosystems on moist forest sites. On dry forest sites, their strategy called for silvicultural treatments that retain and release older trees, reduce stand densities, shift composition toward fire- and drought-tolerant tree species, and incorporate spatial heterogeneity at multiple spatial scales (Franklin and Johnson 2012). The framework included an extensive set of large patches of dense forests on approximately 30 percent of the forested landscape to retain some suitable forest for spotted owls while reducing the potential for landscape-level high-severity wildfires.

DellaSala et al. (2013) identified seven areas in which the ecological forestry framework may fall short of the stated goals of the NWFP, and offered 14 recommendations to improve the framework and its implementation. They also criticized decisions to incorporate some of the elements of ecological forestry in the revised recovery plan and revised critical habitat designation. Henson et al. (2013) agreed with many of the recommendations made by DellaSala et al. (2013), but differed on two key perspectives. Henson et al. (2013) regarded the potential impacts of wildfire to spotted owls as higher risk to species persistence, and suggested that in many circumstances, the adverse effects associated with active management may be preferable to adverse effects of passive management. As with wildfire risk, the fundamentals of this debate reside in philosophical disagreements about ecological goals and what role active management should play in managing public lands. Most research in dry or frequent-fire forest landscapes suggests that active management is needed to achieve or accelerate restoration objectives, but more study is needed to advance our understanding of disturbance effects on wildlife dependent on old forest, especially interactions between wildfire and a range of prefire and postfire active management actions.

Modeling to inform critical habitat designation—

The Fish and Wildlife Service (USFWS 2012a) produced maps of distribution of potentially suitable habitat for spotted owls that did not include the effects of barred owls on spotted owl distribution, but the effort did incorporate the spatial arrangement of forest structure associated with nesting/roosting and foraging, and abiotic factors such as slope and topographic position, to determine the extent of critical habitat. In an alternate analysis, Loehle et al. (2015) conducted an accuracy assessment of vegetation data used as input to develop the USFWS (2012a) models, used independent locations to validate model prediction, correlated model output with spotted owl reproductive success in two study areas, and developed alternate models. Their independent locations and vegetation evaluations suggested a high rate of classification errors, and productivity did not correlate well with predictions in their study areas (Loehle et al. 2015). Dunk et al. (2015) defended the critical habitat model as scientifically rigorous and as meeting the goals established by the Fish and Wildlife Service. They suggested that Loehle et al. (2015) mischaracterized the literature and the Fish and Wildlife Service species distribution model, failed to demonstrate the locations used by the agency were biased, and failed to show significant flaws in analytical methods.

Bell et al. (2015) argued that Loehle et al. (2015) underestimated the predictive performance of critical habitat maps because the field plots they used potentially biased the accuracy assessment toward older forests, and that they examined accuracy at finer scales than the model was intended to predict. Loehle and Irwin (2015) responded to Bell et al. (2015) and Dunk et al. (2015) by arguing that, although the habitat models average out at large spatial scales, errors at smaller scales may limit their utility for conservation. This debate underscores the importance of acknowledging the appropriate scale at which predictive distribution models can be used for conservation purposes. The debate also serves as another example highlighting the need to recognize and carefully evaluate how habitat is defined. The definition of habitat for spotted owls must now consider that forests that were once suitable for spotted owls are less suitable habitat if occupied by barred owls.

Conclusions and Management Considerations

Spotted owls are a resilient subspecies but are faced with significant challenges. Research and monitoring efforts over the past several decades have documented the population declines and risks to spotted owls despite measures to address their long-term sustainability. The framework, standards, and guidelines of the NWFP have been both critical and necessary for spotted owl conservation, and underlie species recovery plans. However, because of barred owls and continued forest perturbations outside of federal lands, the NWFP alone is not sufficient for spotted owl recovery. Additional measures beyond the Plan will be needed for long-term persistence of spotted owls. Suitable habitat continues to decline because of current and lingering effects of extensive forest disturbance, and the recent invasion of a formidable congeneric competitor has reduced the space available for spotted owl recovery. The need to provide habitat for spotted owls has been a critical component of conservation plans and was a major catalyst for developing the NWFP. It is now clear that barred owl presence reduces habitat suitability for spotted owls, so species recovery will require protections for old forest and management actions focused on reducing the threat from barred owls. After only two decades, it is too early to evaluate if the Plan has been effective at improving the conservation status of spotted owls; however, the framework, standards, and guidelines of the NWFP have aided spotted owl conservation; if logging had continued at pre-NWFP levels, spotted owl populations certainly would have declined more rapidly over the past 20 years. Further, the NWFP has put federal lands on a trajectory for providing enough suitable forest for recovery of spotted owl populations over the next several decades. The effectiveness of LSRs established under the NWFP is linked to the frequency, severity, spatial extent, and type of disturbance, as well as how those disturbances are offset by recruitment of suitable forest, primarily through succession. Disturbance events can reduce the suitability of forests used by spotted owls for several decades by creating open canopy conditions and reducing structural complexity. Although disturbance rates have exceeded suitable forest-cover

recruitment rates during the first 20 years of the NWFP, recruitment will likely outpace losses if current timber harvests and wildfire occurrence remain constant. However, climate models suggest that wildfire occurrence may increase, causing significant reductions in cover for spotted owls, and that suitable forest cover for spotted owls will move northward and occur at higher elevations. Therefore, other reserves designated before development of the NWFP, such as parks and wilderness areas, may become increasingly important for spotted owl conservation.

Several lines of compelling evidence indicate that interspecific competition between spotted owls and barred owls is causing accelerated population declines of spotted owls, despite widespread conservation of old forests under the NWFP. Competitive pressure from barred owls may negate the benefits of recruitment of suitable forest cover, because barred owls exclude spotted owls from sites that otherwise are suitable for spotted owls. It remains uncertain how, or if, spotted owls can coexist with barred owls. Although much research has been done on spotted owls, we identified many uncertainties in available information and have identified future research needs important for management of the subspecies. The long-term effects of barred owls and fine-scale partitioning of resources remain unknown, and studies are needed to identify resilient sites for spotted owls in the face of competitive interactions with barred owls, if they exist. Additionally, it remains unknown how, or if, spotted owls will respond to removals of barred owls from historical spotted owl territories.

Abundance and distribution of primary prey species can influence home range size and forest selection by spotted owls. But it remains unknown how spatially and temporally fluctuating prey populations influence the survival and reproduction of spotted owls. Studies are needed to quantify relationships between interannual fluctuations in prey abundance and long-term demography of spotted owls. The short- and long-term effects of silvicultural treatments and wildfire on spotted owl occupancy, forest dynamics, and prey remain unclear. The optimization of forest restoration and conservation of spotted owls will require more knowledge about the conditions under which restoration activities can benefit spotted owls in the long term without significant detrimental impact in the short term.

Management Considerations

Forest management and barred owls—

Wiens et al. (2014) found that adult survival of spotted owls and barred owls was higher in home ranges with greater amounts of conifer forest dominated by trees age 120 years or older. Dietary studies also showed that barred owl diet is broader than spotted owls, but both owl species relied on similar prey associated with older forest types (e.g., northern flying squirrels and red tree voles). These findings have important implications for land managers because they suggest that (1) conservation of old forest under the NWFP not only promotes survival of spotted owls, but also survival of barred owls; and (2) availability of old forests (and associated food resources) is a key limiting factor in the competitive relationship between the two owl species (Wiens et al. 2014). As barred owls continue to increase in number, it has become clear that conservation of the spotted owl and its forest cover types need to be extended from ameliorating the effects of old-forest loss and fragmentation to accounting for the impacts of a widespread invasive competitor as well. Although spotted owls are known to use recently thinned stands (e.g., Irwin et al. 2015), it remains unclear how such silvicultural treatments can affect the fitness of spotted owls in the long term or how barred owls may respond to those management actions. Those silvicultural treatments with high disturbance likely increase long-term extinction rates of spotted owls by reducing forest complexity and thus suitability for spotted owls but not necessarily for barred owls (Dugger et al. 2016, Singleton 2015, Singleton et al. 2010, Sovern et al. 2014, Wiens et al. 2014).

Barred owl densities may now be high enough across the range of the spotted owl that, despite the continued management and conservation of suitable forest cover types under the NWFP, the spotted owl population will continue to decline without intervention to reduce barred owl populations (Dugger et al. 2016). Recommendations to conduct experimental removal of barred owls to benefit spotted owls have been criticized as being too difficult to accomplish owing to the effort and cost required to maintain sufficiently low numbers of invasive barred owls (Livezey 2010, Rosenberg et al. 2012). Nonetheless, experimental removal of barred owls on one study area in California suggests that

removal of barred owls may have positive, short-term effects on population trends of spotted owls (Diller et al. 2016, Dugger et al. 2016). In 2013, the Fish and Wildlife Service decided to expand removal experiments to additional sites in California, Oregon, and Washington to determine if similar results can be obtained in areas with different forest conditions and densities of barred owls (USDI 2013, USFWS 2013). Those experiments will yield information about how spotted owls respond, and will convey the economic and logistic feasibility of removal efforts as potential management actions. Such information will be useful in projecting possible long-term consequences and benefits of an active management program for barred owls in the future.

Current evidence suggests that a combination of habitat protection and active management of barred owls are the two highest priorities for stabilizing declining trends in populations of spotted owls. A recent analysis casts doubt on the likely effectiveness of barred owl removals for spotted owl conservation (Bodine and Capaldi 2017). Experimental culling of barred owls will provide information to validate those models and about how, or if, their populations can be controlled at scales sufficient to promote recovery of spotted owls. However, detailed studies of habitat associations and resource use by barred owls have been conducted in only a few limited areas within the range of the spotted owl. More detailed studies in other areas will better enable an understanding of how specific tree species, stand densities, or physiographic conditions are negatively associated with barred owls but not spotted owls.

Wildfire and active management—

Disturbance processes that increase forest or landscape heterogeneity (e.g., wildfire, management activities) can benefit spotted owls as long as the required forest structural conditions are available for foraging, nesting, and roosting activities. Processes that substantially simplify stand structure or landscapes often have negative impacts on the suitability of forest for spotted owls. Our basic understanding of forest structural conditions used by spotted owls has not substantially changed over the past 20 years, but there has been a growing recognition of the contribution of diverse forest conditions to broader ecosystem function and species diversity in conifer forests of the Pacific Northwest. This is especially true in historically moderate- and high-frequency

fire regime landscapes where fire suppression and forest management have greatly reduced fire and altered forest structure and composition at stand and landscape scales (chapter 3). For example, nonconiferous vegetation, including shrubs and broad-leaved trees, makes an important contribution to the diversity of forest landscapes. Therefore, allowing shrubs and hardwood trees to develop and persist in early-seral stands, and curtailing vegetation control, will benefit many wildlife species associated with nonconiferous vegetation (Hagar 2007), including some spotted owl prey species (Diller et al. 2012). Additionally, diversity and configuration of different forest types are important for spotted owls at stand, home range, and landscape scales (Franklin et al. 2000). The function and diversity of an ecosystem is enhanced by the presence of high-quality early-seral patches (i.e., a mix of nonforest and forest) because they have high species and structural diversity (Swanson et al. 2011). These early-seral ecosystems can be created using low-intensity approaches for regeneration, combined with retention of biological legacies to promote the development of structurally diverse closed-canopy forest over time (Franklin and Johnson 2012). Indeed, under normal conditions, natural disturbances frequently result in patches of high-quality early-seral ecosystems, provided that intensive salvage and replanting does not occur after the disturbance (Swanson et al. 2011).

Disturbances have different impacts on spotted owls depending on the scale under consideration. A hypothesis that has emerged from recent research is that disturbance processes (e.g., low- and mixed-severity wildfire, light to moderate thinning) that increase stand or landscape heterogeneity can have long-term benefits for spotted owls, as long as enough suitable forest cover for nesting and roosting remain within the territory. Conversely, disturbances that substantially simplify stands or landscapes often have long-lasting negative impacts on spotted owls and their habitat. Finally, we emphasize the importance of conserving sites currently occupied by spotted owls as well as those that are known to have been historically occupied by the subspecies. Many sites, for example, have been abandoned as a result of disturbance to suitable forest cover or displacement by barred owls, but maintain structure suitable for nesting and roosting. Those remaining spotted owls and sites likely

represent unique behavioral or forest characteristics that may not yet be fully recognized, thus they are an important research need. Conserving the unique forest structural conditions of those few sites that remain, particularly in the northern portion of the geographic range, will likely have a positive benefit for the long-term persistence of spotted owls.

Prognosis for the future—

In the 2011 revised recovery plan for spotted owls, the Fish and Wildlife Service’s modeling team used the HexSim modeling program (Schumaker 2008) to simulate population-level responses to various conservation strategies and other threats (USFWS 2011b). They developed models based on demographic data (Forsman et al. 2011), dispersal information (Forsman et al. 2002, Thomas et al. 1990), and home range size (Carey et al. 1990; Forsman et al. 1984, 2005; Glenn et al. 2004; Hamer et al. 2007). Objectives of the modeling effort were to (1) evaluate if future viable

populations of spotted owls were likely given conditions at the time (demographic rates, LSR network, amount of suitable forest cover, barred owls); (2) estimate population viability under different conservation networks of suitable forest cover; and (3) quantify the effect of forest cover and barred owl management on recovery goals for spotted owls (USFWS 2011b). The modeling results suggested that availability of suitable forest cover was critical for territory acquisition and sustained occupancy by spotted owls. Population viability models suggest that barred owls reduce spotted owl survival and act to depress populations to about half of potential population size without barred owls (fig. 4-9). Simulations did not include the barred owl impact on spotted owl reproduction, forest selection, site fidelity, or detection probability, and were based upon early rates of population growth. More recent population change estimates (Dugger et al. 2016) indicate a further declining growth

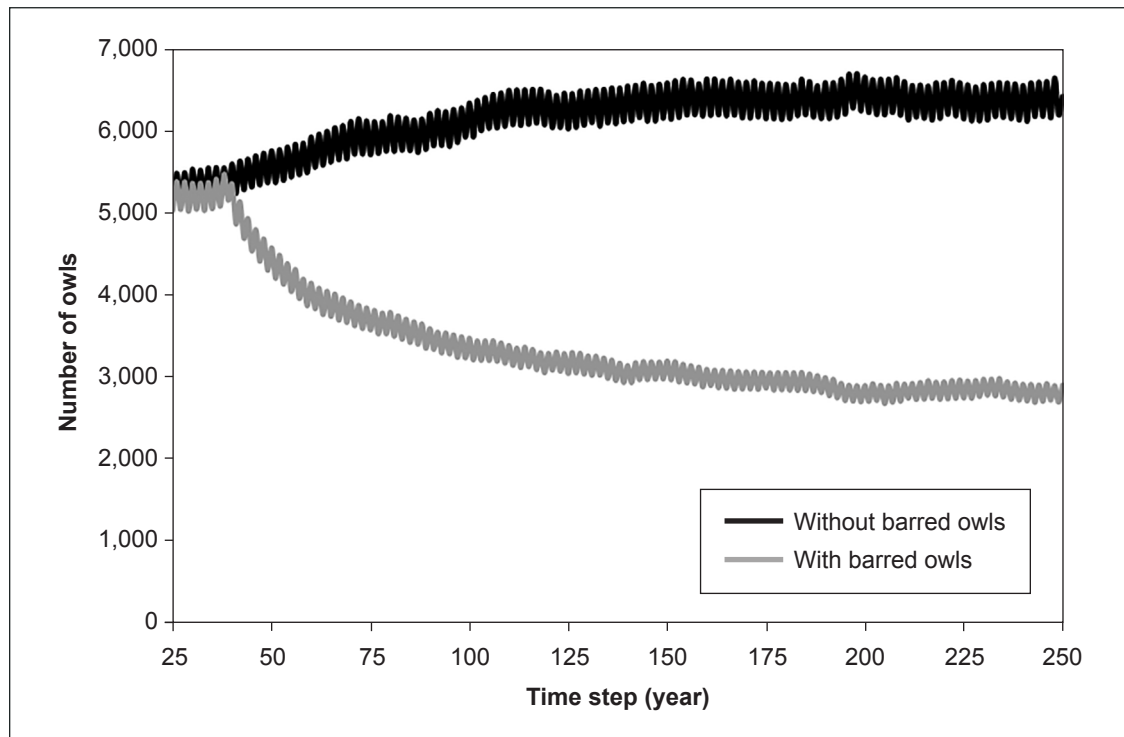


Figure 4-9—HexSim model runs with five replicates each for without barred owl impacts and with barred owl impacts for the spotted owl’s geographic range in the United States. The apparent within-year variation that appears in the figure is a function of an “even-odd” year effect on reproduction (USFWS 2011b). The first 30 years of the simulation was a “burn-in” period, which provided for the simulated population to distribute according to available resources and develop an age structure determined by demographic processes. Barred owl effects were not included during the “burn-in” period and were introduced starting at year 30 (USFWS 2011b).

rate, suggesting that USFWS (2011b) projected estimates are more optimistic than what is likely to be observed in spotted owl populations. These studies provide further evidence that the framework, standards, and guidelines of the NWFP are critical components to spotted owl recovery plans, but the impacts of barred owls will likely need to be controlled if spotted owl species recovery is to be successful.

Schumaker et al. (2014) used the HexSim model originally developed by the Fish and Wildlife Service (USFWS 2011b) to simulate and quantify source-sink dynamics and landscape connectivity throughout the range of the spotted owl. Their results indicated that populations are likely to decline in most regions, but that southern Oregon and northern California may serve as source populations. Marcot et al. (2013) also used the HexSim model to evaluate how size and spacing of suitable forest cover types for spotted owls affected simulated population size and persistence. Their results indicated that long-term occupancy rates were significantly higher with suitable forest patches large enough to support 25 spotted owl pairs or more, with less than 9.3 mi (15 km) spacing between patches, and with overall landscapes of at least 35 to 40 percent suitable forest cover types for nesting and roosting. In a sensitivity analysis, Marcot et al. (2015) determined that spotted owl response variables in the HexSim model were most sensitive to the availability of highly suitable forest cover for nesting and roosting. All these studies used static habitat maps that did not incorporate climate change or wildfire impacts on spotted owls. Only the USFWS (2011b) model incorporated effects of barred owls.

Spotted owl populations have continued to decline under the NWFP, but because of slowed timber harvest on federal lands since the late 1980s, forests throughout most of the range of the spotted owl are on a trajectory—through succession—to develop suitable forest characteristics for spotted owls in coming decades. When the NWFP was adopted, spotted owl populations were expected to continue declining for up to 50 years because of lingering impacts of previous losses of suitable forest cover, yet the magnitude and characteristics of barred owl impacts were unknown and unexpected at that time. Per assumptions of the NWFP, we are unable, after only two decades, to use

stable or increasing populations (i.e., improved conservation status) of spotted owls as the success criterion for the NWFP. However, if the success criterion is forests capable of supporting interconnected populations of spotted owls in the absence of barred owls, then the implementation of the framework, standards, and guidelines of the NWFP has put federal lands on a trajectory for success, despite recent losses of suitable forest cover to wildfire. In the Pacific Northwest, forest succession from early-seral to climax forest is a slow process, which is in part the reasoning for the NWFP to be a 100-year plan intended to span several human generations (USDA and USDI 1994). Further, conservation and management of spotted owls rests critically on continued implementation of the protections afforded by the NWFP and the Endangered Species Act (Noon and Blakesley 2006). It also rests on improving our understanding of how to minimize impacts of barred owls, and on fine-tuning our ability to retain needed forest structure while also increasing resiliency of forests through strategic management.

U.S. and Metric Equivalents

When you have:	Multiply by:	To get:
Inches	2.54	Centimeters
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres

Acknowledgments

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Marbled murrelet.
Photo by Kim Nelson, Oregon State University.